The greening of Western Australian landscapes: the Phanerozoic plant record

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Abstract

Western Australian terrestrial floras first appeared in the Middle Ordovician (c. 460 Ma) and developed Gondwanan affinities in the Permian. During the Mesozoic, these floras transitioned to acquire a distinctly austral character in response to further changes in the continent's palaeolatitude and its increasing isolation from other parts of Gondwana. This synthesis of landscape evolution is based on palaeobotanical and palynological evidence mostly assembled during the last 60 years. The composition of the plant communities and the structure of vegetation changed markedly through the Phanerozoic. The Middle Ordovician – Middle Devonian was characterised by diminutive vegetation in low-diversity communities. An increase in plant size is inferred from the Devonian record, particularly from that of the Late Devonian when a significant part of the flora was arborescent. Changes in plant growth-forms accompanied a major expansion of vegetation cover to episodically or permanently flooded lowland settings and, from the latest Mississippian onwards, to dry hinterland environments. Wetter conditions during the Permian yielded water-logged environments with complex swamp communities dominated by *Glossopteris*. In response to the Permian–Triassic extinction event, a transitional vegetation characterised by herbaceous lycopsids became dominant but was largely replaced by the Middle Triassic with seed ferns and shrubs or trees attributed to *Dicroidium*. Another floristic turnover at the Triassic–Jurassic boundary introduced precursors of Australia's modern vegetation and other southern hemisphere regions. Most importantly, flowering plants gained ascendancy during the Late Cretaceous. Characteristics of the state's modern vegetation, such as sclerophylly and xeromorphy, arose during the Late Cretaceous and Paleogene. The vegetation progressively developed its present-day structure and composition in response to the increasing aridity during the Neogene–Quaternary.

Keywords: palaeobotany, palynology, vegetation, palaeoclimate, Western Australia

INTRODUCTION

Terrestrial vegetation of the geological past can be reconstructed using molecular, micro- and megascopic fossil remains. This article focuses mainly on palynological and palaeobotanical material corresponding to the 'micro-' and 'megascopic' remains preserved in the fossil record. Although outside the scope of this paper, molecular biogeochemical studies of fossil plants are increasingly significant in understanding the evolution of plant life (Spaak *et al.* 2017). Although a substantial amount of palynological information can be obtained from publicly available reports commissioned by petroleum industries and governmental institutions, the majority of data considered herein is from published sources. As study techniques and the results obtained depend on the nature and size of the material examined, this article initially addresses methodological aspects. For each time interval, representative palynological and megafloral assemblages of the terrestrial flora are discussed and their most significant representatives illustrated. General tectonic and geological settings are illustrated in Figure 1, and locality information is
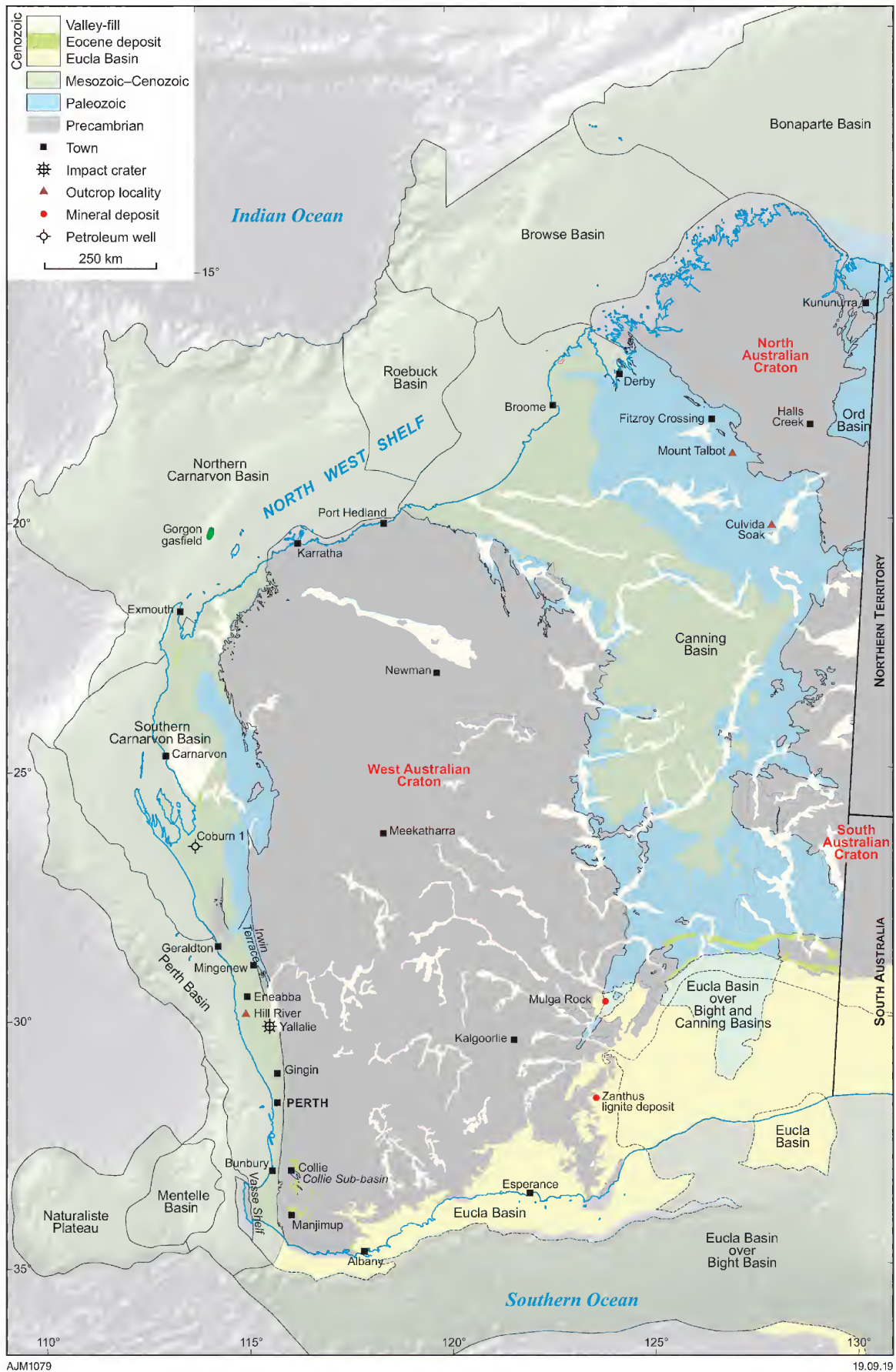
Figure 1. Onshore and offshore Western Australia showing major tectonic elements and localities cited in text.

listed in Appendix 1. Figures 2–8 include type material housed in the collections maintained by the School of Earth Sciences of The University of Western Australia (UWA), the Western Australian Museum (WAM), the Australian Museum (AMF) and the Swedish Museum of Natural History (NRM). Significant contributions to this paper include those from CF and GP on the Ordovician–Devonian; JB, CF, GP and SMcL on the Carboniferous–Permian; DJM and SMcL on the Triassic–Jurassic; and RJC and LAM on the Late Cretaceous – Holocene. Full names of taxa are provided in Appendix 2.

Classification and preservation of plant fossils

Fossilised plant remains initially can be grouped according to size: miospores, which are less than 200 µm in diameter; mesofossils, which include megaspores and 0.2 – 5 mm plant fragments; and larger remains, usually termed megafossils (or macrofossils).

The term miospore collectively embraces spores from non-flowering plants and fungi, and pollen grains (aka pollen) from both flowering and non-flowering plants. Spores are organic-walled, commonly with distinctive shapes, unicellular or multicellular reproductive bodies associated with sexual reproduction in land plants and asexual reproduction in fungi. In land plants, spores are the result of a final meiotic division. They are further categorised according to their size and morphological characteristics. Isospores and microspores represent small (commonly <200 µm) unicellular, dispersal units produced by homosporous plants (mosses, most ferns) and heterosporous plants (quillworts, water ferns, *Selaginella*), respectively. Megaspores are larger dispersal units produced by heterosporous plants. Despite having similar functional characteristics to micro- and isospores, megaspores (usually >200 µm) are often excluded from routine palynological analyses, which tend to focus on smaller and commonly more abundant plant microfossils. Pollen are the male counterparts of the ovules and represent the microgametophyte generation of seed plants (Chaloner 1970). Miospores characteristically have a highly durable organic external wall, which includes the chemically inert biopolymer sporopollenin. General introductions to pollen and spores are too numerous to be listed here. Enthusiasts may find instructive the superbly illustrated book *Pollen* (Kesseler & Harley 2008). Undergraduate and postgraduate students will find authoritative compendia in the three volumes edited by Jansonius & McGregor (1996); the second edition of *Paleopalynology* (Traverse 2007); and in *Quaternary palynology* (Moore *et al.* 1991; focused on Holocene palynomorphs).

Mesofossils include relatively small plant fragments and large megaspores. The former comprise conductive tissues, cuticles, roots, stems, leaves, fruits or any other plant debris <5 mm in diameter. The nature of the recovered assemblage is largely dependent on depositional and diagenetic processes. The initial biochemical composition of the plant remains will influence their abundance in the stratigraphic record. In particular, the presence of the extremely stable organic polymers lignin and cutin, which strengthen cell walls and form a chemically stable component of plant cuticles

respectively, greatly enhances their preservational potential in sedimentary facies. Burial under anaerobic conditions (e.g. either in permanently flooded terrestrial mires and swamps, or in marine settings below a stratified water column) may lead to coalification. This process represents a complex series of physical, chemical and structural changes associated with an increase in carbon content and aromaticity, and a concomitant decrease in oxygen and other volatile components. Coalification generates significant changes in colour and physical properties of plant remains that have to be considered during their laboratory extraction and later analysis. More advanced (i.e., higher rank) coalification destroys minute anatomical characteristics such that only gross morphological features may be preserved. Conversely, oxygen-depleted conditions may enhance plant preservation via partial burning or charring to produce fusains, which are highly inert chemically and moderately resistant to degradation by microbial attack—a process sometimes called charcoalification. The presence of charcoalified fossil plant debris has important applications in palaeoenvironmental and climatic reconstructions as it typically signifies episodes of intensive wildfires. Examples of such inferences are the recognition of dry climatic conditions during the Middle to Late Triassic in the Northern Carnarvon Basin (Scibiorski *et al.* 2018) and the expansion of fire-prone sclerophyll vegetation during the Neogene in Western Australia (van der Kaars *et al.* 2000; Atahan *et al.* 2004).

Although various preservational styles of plant megafossils have been recorded (as discussed by, inter alia, Schopf 1975), compression/impression (adpression) and permineralisation (petrifaction) constitute the most common modes of preservation (Chaloner 1999). The former involves transformation during the incorporation of comparatively soft plant fragments within the surrounding matrix and their progressive flattening with increasing depth of burial. Whereas internal structures are usually destroyed by the collapse of the plant tissues, coalification of the organic material forms dark carbonaceous layers that retain the original outline of the plant fragments (Taylor *et al.* 2009). This process can preserve delicate superficial structures (trichomes, stomata) and cuticles, and can create fracture planes separating the organic remains from the mineral matrix. The adjacent mineral layer may retain an exact imprint (mould) of the coalified remains. When such plant fragments have a dorsiventral architecture (as do most leaves), they tend to accumulate more or less parallel to the bedding plane, creating closely stacked layers. Spectacular examples are present within the Permian Irwin River Coal Measures near Mingenew in the northern Perth Basin and in coeval strata at Collie.

In environments characterised by anoxia, acidic conditions and high primary productivity, accumulating plant material can form thick deposits of peat. When plant remains are buried to suitable depths, they undergo a gradual transformation, progressing successively with increasing burial and/or temperature, from lignite to sub-bituminous and bituminous coal, and ultimately to anthracite. The higher ranks of coal (sub-bituminous and above) are typically characterised by plant fragments altered beyond recognition. Although palaeobotanically and palaeoenvironmentally less informative, high-rank

coals are economically important and can contribute to hydrocarbon generation. In Western Australia, economic (and potentially economic) sub-bituminous coalfields have been discovered in the Collie Sub-basin, an eastern outlier of the southern Perth Basin, and in the main part of the basin (Irwin Terrace, Hill River area, Vasse Shelf). Apart from the Lower Jurassic Cattamarra Coal Measures near Hill River and Eneabba, these coal measures contain Permian palyno- and megafloras (Backhouse 1991; Hocking & Preston 1998). Coalification processes are often associated with the generation of gas, for which Western Australia is particularly notable given its numerous offshore gas fields incorporating some of the world's largest proven reserves (e.g. Greater Gorgon, Scibiorski *et al.* 2018).

As noted above, permineralisation is a common mode of plant fossilisation. During the early phases of diagenesis, mineral-charged groundwater permeates cells and plant tissues, precipitating mineral fractions of varying composition. Silicate or carbonate precipitates are common but other minerals (gypsum, phosphate, fluorides, pyrite, oxides) may be involved in this process. Permineralisation can provide outstanding three-dimensional preservation of cell wall and anatomical structures (Taylor *et al.* 2009). In exceptional cases, this process can even preserve soft parts down to the level of cell nuclei and other organelles (Bomfleur *et al.* 2014). General introductions to palaeobotany aimed at undergraduates, collectors or enthusiasts include the texts by Cleal & Thomas (2009) and Willis & McElwain (2002). More expansive and detailed palaeobotanical treatises are those of, inter alia, Stewart & Rothwell (1993) and Taylor *et al.* (2009).

Techniques of extraction

Appropriate methods of extraction depend on the type and chemical composition of the fossils, the nature of the host rock or sediment, the available laboratory facilities and the techniques originally employed to obtain the samples. The extraction of palynological material described by Gray (1965), Phipps and Playford (1984), Wood *et al.* (1996) and Batten (1999) is summarised below. Indurated samples are usually macerated in acid reagents to dissolve the bulk of the mineral components. Hydrochloric and hydrofluoric acids (this with particular care!) are used to remove calcium carbonate and silicate minerals respectively. Oxidation, followed by alkali treatment, is then necessary for removal of unwanted organic debris. Sieving through a Buchner funnel, or 10-micron nylon cloth, possibly accompanied by a brief session of ultrasonic vibration, may be employed to disaggregate amorphous organic matter and remove fine particles. Finally, staining of the residue may prove useful to enhance the optical contrast of palynomorphs. For Neogene–Holocene samples, particularly if unconsolidated, instead of oxidation the workflow usually includes maceration of the residue by a process called acetolysis (Erdtman 1960); this uses 9:1 acetic anhydride and sulphuric acid to remove unwanted cytoplasmic content, pollenkitt and cellulosic polymers.

The next steps are determined by the focus of the intended analysis. Biostratigraphic studies entail transmitted bright-field light microscopy (TLM) of residues mounted on a slide with a coverslip using a mounting medium of suitable durability and refractive index. Palynological residues destined for detailed morphological or ultrastructural analyses by electron microscopy require additional coating with gold, graphite or other conductive media. Among other techniques, transmission and/or scanning electron microscopy (TEM/SEM) can provide excellent details of miospore ultrastructure and morphology (Milne 1998a; Haig *et al.* 2018, figs 2G–I; Figs 7B, C) and have been successfully utilised in palynological research for over 50 years. TEM facilitates ultrastructural characterisation of the walls of fossil spores/pollen with an unrivalled level of detail: Foster & Balme (1994), for example, used TEM to reveal the ultrastructure of the oldest saccate miospore from the Upper Devonian of Western Australia. Milne (1998a) developed a technique to facilitate quick sectioning and precise orientation of the grain, enabling a single fossil grain to be studied in TLM, SEM and ultimately TEM (Figs 7A–D). These techniques, however, involve time-consuming preliminary conditioning of the material (Kennaway *et al.* 2008); in particular embedding, sectioning and staining. For this reason, the use of alternative techniques, such as Focused Ion Beam (FIB) milling, have recently gained favour among some palynologists (Villanueva-Amadoz *et al.* 2012). The use of more advanced transmitted-light techniques enhancing contrast, such as Confocal Laser Scanning Microscopy (CLSM; Feist-Burkhardt & Pross 1998; Peyrot *et al.* 2007) or Phase and Differential Interference Contrast (PC/DIC) microscopies, remain limited largely to projects carried out in academia, given the high price of the optical devices.

Most of the techniques used to study palynological material are also applicable to meso- and megascopic remains. Where the sedimentary rock is fissile, palaeobotanical material can be partially or totally isolated from the surrounding matrix with the use of needle and hammer (Fairon-Demaret *et al.* 1999). Immersion in hot water or hydrogen peroxide may facilitate the disaggregation of weakly consolidated, fossiliferous sediments. In some cases, whole leaves and other plant parts can be floated out with this method. Foliar fossils, even highly fragmented remains, can also yield plant cuticles. These carry important details that can be used for identification purposes, as well as for palaeoclimatic interpretation. Cuticles are usually isolated by soaking leaf remains in weak chromium trioxide solution, hydrogen peroxide or household bleach. The cuticle can then be stained and mounted on a glass slide for microscopic examination. Impression fossils that lack organic preservation can preserve exquisite leaf venation details, which are best interpreted under low-angle illumination. Thin sections and acetate peels are the techniques of choice for anatomical studies of permineralised material. Procedures described in a companion paper (Haig *et al.* 2018) are not reiterated here. Observational techniques vary depending on the scale of the material. Mesofossils and small megafossils are usually studied via low-magnification light, and/or scanning electron microscopy. Thin sections and small sectioned body parts can be examined using TEM, which may benefit from supplementary mineralogical (X-ray diffraction) or geochemical (ICP-MS, inductively coupled plasma-mass spectrometry or other) analyses.

Undergraduate and postgraduate students will find useful information on diverse techniques commonly utilised for the extraction and study of plant mega- and microfossils in the summary provided by Jones & Rowe (1999).

SUMMARY OF PUBLISHED RECORD

Factors influencing the record

The presence of sporopollenin gives miospores an exceptional resistance to post-burial degradation. This, together with the outstanding aero- and hydrodynamic properties of non-animal dispersed miospores, explains their prolific stratigraphic record (in Western Australia from the Middle Ordovician Goldwyer Formation, Canning Basin, to Holocene and historical successions) and their presence in strata that accumulated in a wide range of depositional settings (from deep marine to terrestrial and aeolian). The outstanding physico-chemical durability of spores and pollen means that they are readily recycled (reworked) together with other resistant sedimentary particles. Nonetheless, miospores remain susceptible to oxidation and, to a certain extent, weathering processes (e.g. Cenozoic lateritisation that affected much of the Australian continent). Palynological material is best preserved in, and recovered from, fine-grained, dark-coloured, sedimentary rocks (shale, claystone and siltstone). In Western Australia, the deep weathering profile and extensive leaching explains the poor or nil recovery from surface samples (Balme & Hassell 1962). Hence, for palynological endeavours, there is a reliance on subsurface samples (preferably drillcores) or those from deeply incised terrains. The nature of the sedimentary rock plays an important role in the preservation of megafossils. Finer grain-sizes (mud, volcanic ash) will enhance the fossilisation and allow better preservation of the original plant material as compressions and impressions. Permineralisation depends on very specific depositional circumstances, particularly pore waters saturated in silicates, gypsum, pyrite and/or oxides.

Paleozoic: evolving vegetation and landscapes

ORDOVICIAN–DEVONIAN: FROM EARLY TERRESTRIALISATION TO THE FIRST FORESTS

The earliest land plant spores, known as cryptospores, formed obligate tetrad configurations (Figs 2A, B), and are interpreted as having been produced by small, millimetre-sized plants related to modern liverworts (Steemans & Wellman 2004). Their oldest records date back to the Middle Ordovician (c. 469 Ma) in Argentina (Rubinstein *et al.* 2010) and Sweden (Rubinstein & Vajda 2019), which pre-dates the Western Australian record by a minimum of 2–12 Ma (Foster *et al.* 2018). The oldest cryptospores found in Western Australia, including *Velatitetras laevigata* (Fig. 2A), are from the Middle Ordovician Goldwyer Formation of the Canning Basin (Spaak *et al.* 2017). These strata were deposited

in a broad, shallow epeiric sea where the earliest land plants grew on emergent banks and would have provided the first greenish tinge to the land surface of Western Australia. Younger records of the cryptospore *Tetrahedraletes medinensis*, possibly of Late Ordovician to Silurian age, have been recovered from the Mallowa Salt, Carribuddy Group, Canning Basin (Foster & Williams 1991). Currently, there are no other Australian Ordovician cryptospore records beyond the Canning Basin.

Western Australian Silurian successions have been the subject of relatively sparse palynological characterisation by Gorter *et al.* (1994) and Backhouse (in Yasin & Mory 1999). Both reported (but did not figure) cryptospores, including *Tetrahedraletes medinensis*, together with rare trilete spores and acritarchs, from petroleum exploration wells in the Southern Carnarvon Basin. More palynological work is required, as coeval strata in Victoria contain one of the oldest known lycopsids (*Baragwanathia longifolia* Lang & Cookson 1935). These herbaceous plants, related to modern clubmosses, produced trilete spores and consisted of photosynthetic, vascularised, decimetric, erect stems bearing elongate leaves in tight helices. The reduction from tetrad unit to a monad trilete spore might arguably have conferred better dispersal capabilities for the reproductive units. However, it is well established that the acquisition of a more robust vascular system effectively enhanced support and water/nutrient conductive capabilities, allowing these plants to colonise a wider range of terrestrial habitats.

Devonian successions are relatively well represented in Western Australian outcrop and subsurface sections, and have been described from the Carnarvon and the Canning basins. Spore assemblages from the Gneudna Formation (Southern Carnarvon Basin)—described in detail by Balme (1962, 1988)—can be considered as representative of the early Late Devonian terrestrial palynoflora of Western Australia. The palynoflora is relatively diverse (up to 45 miospore species) and is dominated by *Geminospora lemurata* (Figs 2C, D), together with significant numbers of other cosmopolitan species, such as *Rhabdosporites langii* (Fig. 2E), *Verrucosisporites scurrus* (Fig. 2F), *Emphanisporites annulatus* (Fig. 2G), *E. rotatus* (Fig. 2H), *Gneudnaspora divellomedia* (Fig. 2I) and *Ancyrospora langii* (Fig. 2J). The presence of the last two species is particularly notable as it highlights a substantial increase in diversity of spore morphologies. *Gneudnaspora divellomedia* is a hilate spore, a relatively uncommon apertural type, and *Ancyrospora langii* bears anchor-like processes reminiscent of those present in modern water fern spores. The record of these spores in the Gneudna Formation and other deposits in the Canning Basin indicates the presence of heterosporous land plants in Australia during the Late Devonian. Heterospory presents significant evolutionary advantages and has been recorded in at least six distinct lineages of land plants during the Devonian (Bateman & DiMichele 1994). Relationships between dispersed miospores and their parental plants are often difficult to establish. However, several lines of evidence indicate that the spores *Geminospora lemurata* and *Rhabdosporites langii* were produced by progymnosperms (Balme 1995), a group considered to include the first arborescent plants. As such, the Gneudna Formation's spore content is
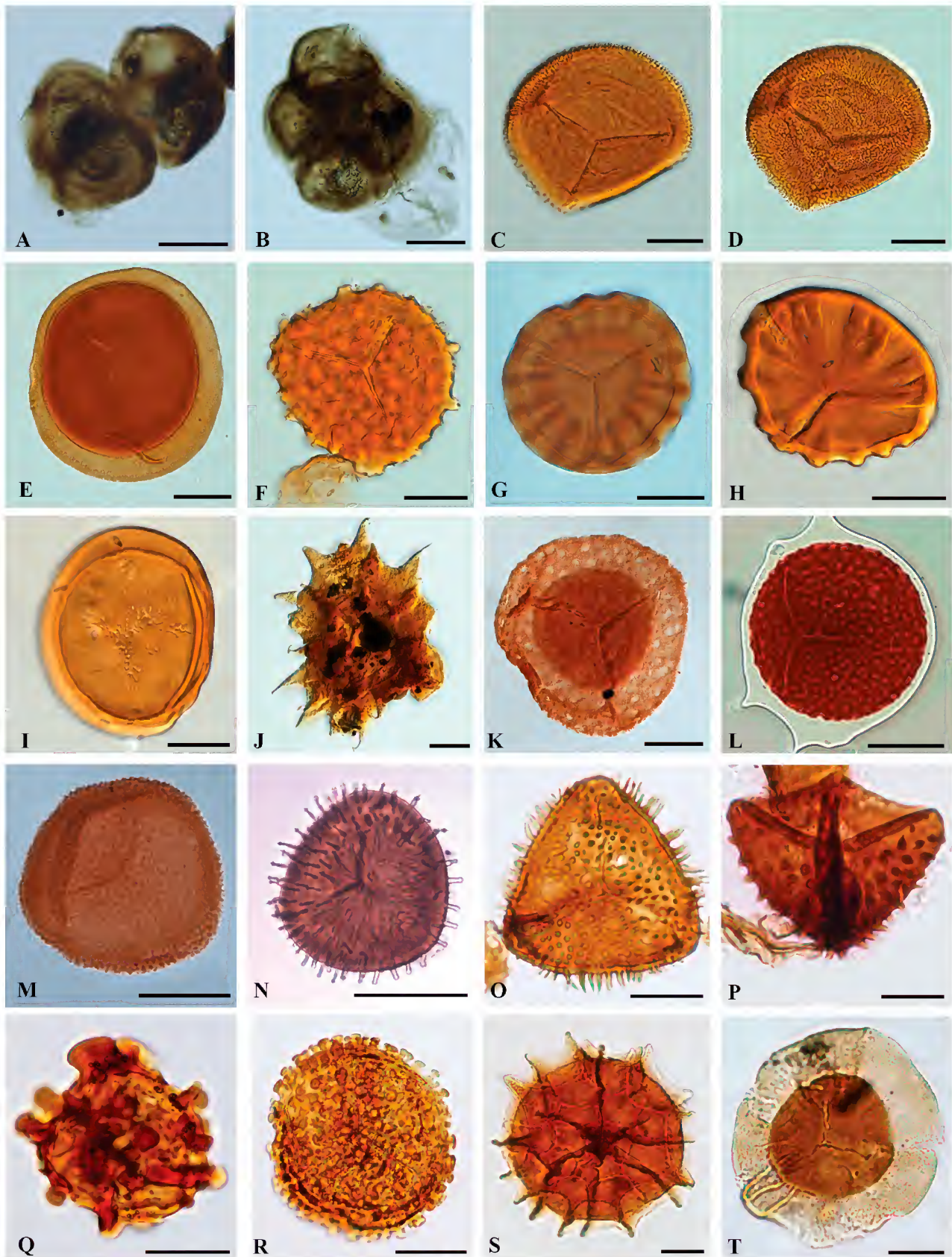
Figure 2. Representative early and later Paleozoic spores from Western Australia: A *Velatitetras laevigata*; B indeterminate cryptospore; C, D *Geminospora lemurata*, proximal and medial foci; E *Rhabdosporites langii*; F *Verrucosisporites scurrus*; G *Emphanisporites annulatus*; H *Emphanisporites rotatus*; I *Gneudnaspora divellomedia*; J *Ancyrospora langii*; K *Retispora lepidophyta*; L *Convolutispora fromensis*, holotype, UWA-45113; M *Granulatisporites frustulentus*, holotype, UWA-45119; N *Claytonispora distincta*; O *Diatomozonotriletes birkheadensis*; P *Anapiculatisporites amplus*; Q *Raistrickia accincta*; R *Raistrickia corymbiata*, holotype, GSWA-F53066; S *Reticulatisporites magnidictyus*; T *Auroraspora solisorta*. Scale bars: 20 μm. Ages: A, B, Ordovician; C–M, Late Devonian; N–T, Carboniferous. See appendices for additional information.

considered representative of swamp, alluvial plain or riparian vegetation that included the first trees in Western Australia during the early Late Devonian. By the latest Devonian, the state's vegetation experienced a near-complete turnover as shown by the substantially different spore assemblages preserved in uppermost Devonian and lower Mississippian strata of the Canning and Bonaparte basins. These assemblages include elements belonging to the cosmopolitan *Retispora lepidophyta* palynoflora, which includes, together with the eponymous species (Fig. 2K), certain taxa that are recorded elsewhere in coeval successions (Playford 1976, 1982). Some of Western Australia's oldest plant megafossils, represented by tree-sized lycopsid (lepidodendrid) stem casts and impressions are preserved in uppermost Devonian strata of the Kellys Knob Sandstone, Bonaparte Basin, east of Kununurra (Fig. 4A).

CARBONIFEROUS–PERMIAN: INCEPTION, PROLIFERATION AND DEMISE OF GONDWANAN SWAMP FORESTS

Mississippian

Megascopic plant remains are extremely scarce in the Carboniferous strata of Western Australia (McLoughlin & McNamara 2001), being limited to a few herbaceous and short-stature lycophytes recovered from the Southern Carnarvon and Canning basins. By contrast, the palynological assemblages of this age in Western Australia are diverse and well-characterised for the Canning Basin (Playford 1976), Bonaparte Basin (Playford 1971; Playford & Satterthwait 1985, 1986, 1988; Satterthwait & Playford 1986), and, more recently, for the Carnarvon and Perth basins (Quail Formation and/or lateral equivalents, Playford 2015; Playford & Mory 2017).

The Mississippian palynofloral succession has been subdivided into various palynostratigraphic units, the oldest being the Tournaisian–Visean *Granulatisporites frustulentus* Microflora (Kemp *et al.* 1977). That assemblage, so named as it is dominated by this species (Fig. 2M), includes elements present in the Famennian (latest Devonian), such as *Convolutispora fromensis* (Fig. 2L), together with cosmopolitan and stratigraphically more restricted species, such as *Claytonispora distincta* (Fig. 2N). Kemp *et al.* (1977) indicated a broad correspondence between this palynoflora and a *Lepidodendron* (Mega-) Flora on the basis of palynological correlations between eastern and Western Australian basins.

Younger Mississippian assemblages (mid-late Visean – early Serpukhovian, Mississippian), comprehensively described by Playford (2015) and Playford & Mory (2017) from the subsurface of the northern Perth and the Carnarvon basins, are relatively diverse (up to 45 species). These assemblages include the typical Gondwanan elements *Reticulatisporites magnidictyus* (Fig. 2S), *Grandispora maculosa* (Fig. 3A), *Psomospora detecta* (Fig. 3B), *Anapiculatisporites amplus* (Fig. 2P), *Indotriradites daemonii* (Fig. 3C), *Velamisporites cortaderensis* (Fig. 3E) and *Verrucosisporites quasigobbettii* (Fig. 3F), together with cosmopolitan species, such as *Anapiculatisporites concinnus* and *Auroraspora solisorta* (Fig. 2T).

In Western Australia spores with a more restricted geographic distribution and stratigraphic range include *Raistrickia accincta* (Fig. 2Q), *R. corymbiata* (Fig. 2R), *Diatomozonotriletes birkheadensis* (Fig. 2O), *Indotriradites kuttungensis* (Fig. 3D) and *Spelaeotriletes ybertii* (Fig. 3G). Collectively, these suites indicate an increasingly Gondwanan, less cosmopolitan flora. In eastern Australia, this assemblage is associated with the *Nothorhacopteris argentinica* Flora of Retallack (1980).

Upper Serpukhovian (uppermost Mississippian) and younger strata incorporate the first pollen (aka prepollen). These bilaterally symmetrical monosaccate pollen (of the genus *Potonieisporites*) were produced by early representatives of Voltziales, an extinct late Paleozoic group of arborescent gymnosperms distantly related to modern-day conifers. Together with radiosymmetric monosaccates, these pollen progressively assumed a major role in the palynological successions of this interval in Western Australia and elsewhere in Gondwana. The inception of gymnosperms (and their ensuing radiation through the Pennsylvanian) marks the most significant palaeofloristic event prior to the introduction of angiosperms in the Early Cretaceous.

Pennsylvanian–Permian

The Pennsylvanian is characterised by major global cooling, leading to the establishment of an extensive ice sheet covering the bulk of Eastern Gondwana, including much of the region corresponding to Western Australia (Mory 2017; Martin *et al.* 2019). As a result, Pennsylvanian strata are poorly represented in the state and have been intersected by only a few wells, mainly in the northern Canning (Powis 1984; Apak & Backhouse 1999) and Bonaparte basins (Mory 2017). The palynofloras of this later Carboniferous are characterised by abundant monosaccate pollen—*Plicatipollenites* spp. (Fig. 3H) and *Potonieisporites* spp. (Fig. 3I)—and impoverished spore associations including the lycopsid element *Cristatisporites* and spores of uncertain affinities, such as *Calamospora* spp. (Fig. 3J), *Punctatisporites gretensis* (Fig. 3K) and *Secarisporites* spp. (Fig. 3L). The palynofloral assemblages of this interval have been linked to the *Sphenopteridium* (=*Fedekurtzia*) Flora described in eastern Australia (Retallack 1980; Coturel & Césari 2017).

Icehouse conditions of the Pennsylvanian ameliorated during the Cisuralian (Early Permian). Glacial meltwaters formed lakes and deposited thick mudstones that underlie younger sediments in almost all Phanerozoic sedimentary basins across Western Australia and elsewhere in much of Gondwana. The Permian is characterised by coal in most of the major basins of Western Australia, but thick (economically significant) deposits are confined to the southern Perth Basin (Hocking & Preston 1988). Given their known or prospective economic significance (Collie Sub-basin and Vasse Shelf) and/or good exposure (Irwin Terrace, northern Perth Basin), the coal-bearing successions have been the subject of numerous studies dealing with their spore-pollen (Balme & Hennelly 1955, 1956a, 1956b; Backhouse 1991) and megafloral content (Rigby 1966, 1993; McLoughlin 1992a, 1992b, 1993, 1995; McLoughlin & McNamara 2001).

The Collie Sub-basin's palynoflora is highly diverse (>100 species) and records the radiation of taeniate
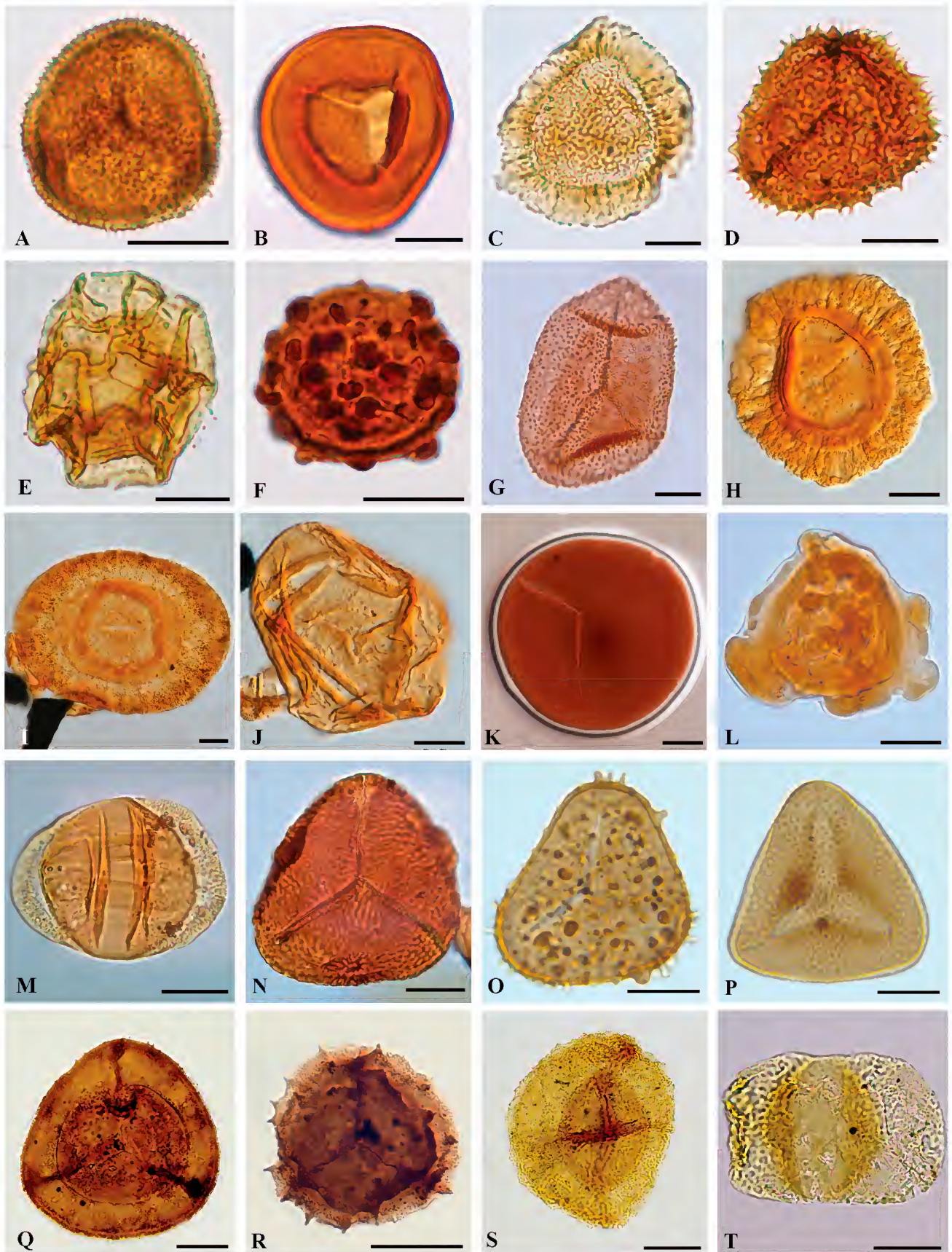
Figure 3. Representative late Paleozoic and early Mesozoic spores and pollen from Western Australia; A *Grandispora maculosa*; B *Psomospora detecta*; C *Indotriradites daemonii*; D *Indotriradites kuttungensis*; E *Velamisporites cortaderensis*; F *Verrucosisporites quasigobbettii*; G *Spelaeotriletes ybertii*; H *Plicatipollenites* sp.; I *Potonieisporites* sp.; J *Calamospora* sp.; K *Punctatisporites gretensis*, holotype, UWA-44984; L *Secarisporites* sp.; M *Protohaploxypinus samoilovichii*; N *Dulhuntyispora parvithola*; O *Horriditriletes tereteangulatus*; P *Microbaculispora tentula*; Q *Lundbladispora willmotii*; R *Kraeuselisporites cuspidus*; S *Aratrisporites banksii*; T *Falcisporites australis*. Scale bars: 20 μm. Ages: A–J, L, Carboniferous; K, N–P, Permian; M, Q–T, Triassic. See appendices for additional information.

pollen grains bearing transverse thickened bands on their proximal side (Backhouse 1991). Such thickened ribs have also been observed in pollen of extant Gnetales (e.g. *Welwitschia mirabilis*) and were interpreted by Foster (1979) as a morpho-functional adaptation to cope with dehydration. Taeniate pollen (e.g. *Protohaploxypinus samoilovichii*, Fig. 3M) are first recorded in Serpukhovian–Bashkirian (uppermost Mississippian – lowermost Pennsylvanian) strata and are frequently observed in Asselian and younger material, thus prompting some authors to recognise the *Striatites* Microflora (Balme 1964; Kemp *et al.* 1977). Early Permian spore associations typically include small ornamented trilete spores assigned to *Cyclogranisporites* spp., *Baculatisporites* spp. and locally abundant *Horriditriletes tereteangulatus* (Fig. 3O). Permian palynofloras also feature spores characterised by a combination of biconvex polar shape, rounded triangular equatorial outline and raised trilete scar. This group, known collectively as the 'cheilocardioid complex', diversified and became quantitatively significant during the Permian (Price & Filatoff 1990). The earliest Gondwanan cheilocardioid spore, *Microbaculispora tentula* (Fig. 3P), evolved during the Pennsylvanian, and the group diversified rapidly as the climate warmed and coal swamps developed throughout Gondwana. Unique to Gondwana, and particularly diverse in the Canning Basin during the Lopingian (Late Permian), are the highly distinctive, presumed fern spores of the genus *Dulhuntyispora* (Fig. 3N); these are regarded as the ultimate development of the cheilocardioid complex (Price & Filatoff 1990).

Permian megafloral assemblages are dominated by relatives of the Glossopteridales including leaves (*Glossopteris*; Fig. 4E), roots (*Vertebraria*; Fig. 4J), reproductive structures (*Arberia, Ottokaria*; Fig. 4B) and wood (*Araucarioxylon*) from gymnosperms up to 30 m tall. These arborescent plants were the main and/or monodominant colonisers of swamps and water-logged lowland settings as represented in the Collie Sub-basin. The megafloras of the Irwin Terrace are somewhat more diverse, including subarborescent and climbing sphenopsids (related to modern horsetails; Figs 4C, D, F, H, L), and low-stature lycophytes and ferns (Fig. 4G). Megascopic remains attributed to Cordaitales (*Noeggerathiopsis*; Fig. 4I) and the seed fern *Bergiopteris* (Fig. 4K), are also found at both locations and have been interpreted as allochthonous; i.e., the transported derivatives of 'upland' vegetation (McLoughlin 1995; McLoughlin & McNamara 2001). The profuse *Glossopteris* flora covered the Western Australian Permian landscape, as indeed throughout the Gondwana supercontinent. However, as the climate warmed and atmospheric conditions deteriorated at the close of the Permian (due to continental-scale volcanism in the northern hemisphere), the extensive *Glossopteris* vegetation vanished and, consequently, the associated striate pollen almost disappeared from the microfossil record. The collapse of this flora preceded, by a few hundred thousand years, the Permian–Triassic extinction event, which affected faunal communities on a global scale (Fielding *et al.* 2019).

Early Mesozoic: changing landscapes and vegetation

TRIASSIC: AUSTRALIAN VEGETATION IN A TIME OF CHANGE

Following the end-Permian mass extinction and the demise of the *Glossopteris* flora, Western Australia experienced prolonged recovery and low plant diversity during the Early Triassic (Retallack 1995a). The Induan–Olenekian plant communities of the Millyit Sandstone and basal Blina Shale in the Canning Basin are dominated by herbaceous lycophytes, such as *Pleuromeia*, along with variable abundances of conifers, sphenopsids and ferns (White & Yeates 1976; Gorter 1978). The Early Triassic spore-pollen associations of the Carnarvon and Perth basins record similar, low-diversity assemblages (Balme 1963; Dolby & Balme 1976; Haig *et al.* 2015) dominated by trilete, cavate lycopsid spores including *Densoisporites*, *Lundbladispora* (Fig. 3Q) and *Kraeuselisporites* (Fig. 3R). Micro- and megafloral attributes suggest a 'recovery flora' featuring abundant opportunistic spore-producers, such as herbaceous lycopsids, ferns (Fig. 5A) and other diminutive plants. This unusual floral physiognomy ('Lilliput effect') has been related to a high concentration of carbon dioxide, extreme chemical weathering and associated greenhouse conditions (Algeo & Twitchett 2010; Retallack *et al.* 2011; Sun *et al.* 2012). The increased nutrient run-off during this interval also led to short-lived episodes of enhanced marine productivity evidenced by recurrent spikes of acritarchs in the palynological record. These are manifest by the prodigious representation of *Micrhystridium* and *Veryhachium* in the Kockatea Shale assemblages of the Perth Basin (Balme 1963; Balme & Foster 1996; Haig *et al.* 2015, 2018). Similarly impoverished Early Triassic plant assemblages are well documented in eastern Australia and across southern Gondwana (Helby 1970, 1973; Retallack 1995b; McLoughlin *et al.* 1997; Vajda & McLoughlin 2007) and may relate to the lack of peat production (the 'coal gap') that persisted globally throughout the Early Triassic (Retallack *et al.* 1996). Initial vegetational recovery during this prolonged aridity in Western Australia began in the late Early Triassic, as shown by increasing diversity of arborescent gymnosperms and shrubby lycophytes; the latter reflected by abundant monolete spores (*Aratrisporites*; Fig. 3S) in palynological assemblages.

Early to early Middle Triassic (Olenekian–Anisian) megafloras from Culvida Soak in the Canning Basin (Retallack 1995a) are of low diversity and dominated by leaves attributed to *Dicroidium*. This foliage was produced by Umkomasiales, an order of seed ferns represented by seasonally deciduous shrubs and trees restricted to Gondwana (McLoughlin 2001; Kustatscher *et al.* 2018), where it is commonly predominant in deltaic megafloras (Retallack 1977). The near-ubiquity of *Dicroidium* in Gondwanan coastal and lowland plant communities until the end of the Triassic is manifested palynologically in Western Australia and elsewhere by its abundant bisaccate pollen *Falcisporites* (Fig. 3T). The remarkably
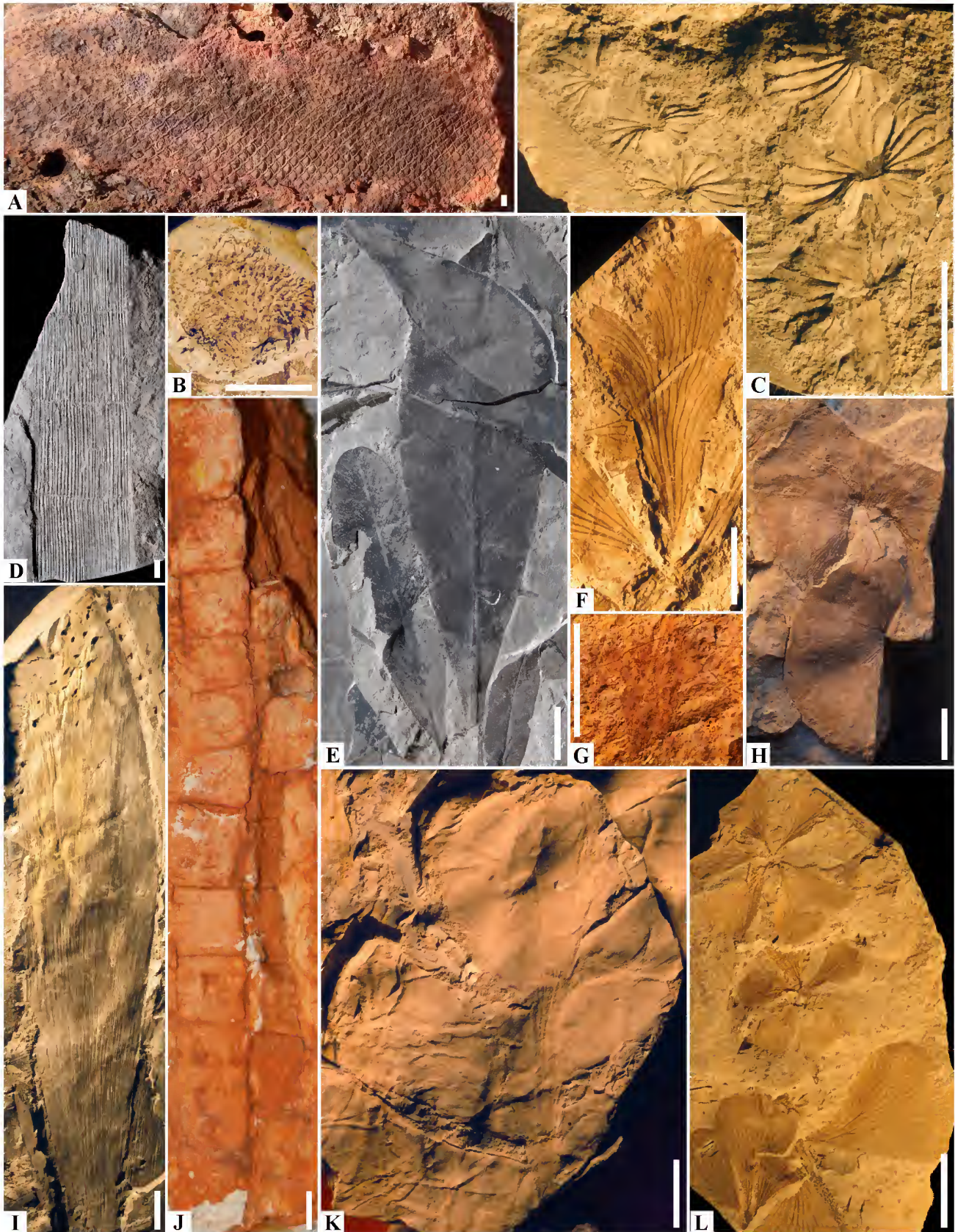
Figure 4. Representative Paleozoic plant megafossils from Western Australia: A Lepidodendroid lycopsid trunk in outcrop; B *Ottokaria bullata* (glossopterid seed-bearing organ), UWA-119121; C *Raniganjia minima* (sphenophyte leaf whorls), UWA-115334; D *Paracalamites australis* (sphenophyte stem), NRM-S048203; E *Glossopteris* sp. (mat of deciduous glossopterid leaves), NRM-S048236; F *Sphenophyllum morganae* (sphenophyte leaflet with reflexed lobes), UWA-115380; G *Liknopetalon* sp. (fertile fern pinnule), WAM-P.86.105; H *Gondwanophyton daymondii* (sphenophyte with fan-shaped leaves), WAM-P.86.58; I *Noeggerathiopsis* sp. (cordaitalean leaf), unregistered specimen; J *Vertebraria australis* (segmented glossopterid root), NRM-S166964; K *Bergiopteris* sp. cf. *B. archangelskyi* (lobed seed fern leaf), UWA-3902.5A; L *Sphenophyllum rhodesii* (sphenophyte leaf whorls), UWA-115434. Scale bars: 10 mm. Ages: A, Late Devonian; B–L, Permian. See appendices for additional information.

cosmopolitan Early Triassic floras were succeeded by increasing provincialism in the Middle and Late Triassic, as the recovery and evolution of new vegetation types intensified, and distinct floral communities developed across Gondwana and Laurasia. The increasingly diverse associations of pteridosperms, ferns, cycads, conifers, ginkgophytes and sphenopsids are best represented in Western Australia by their spore-pollen record (the Onslow Microflora; Dolby & Balme 1976) in the Northern Carnarvon Basin. This latitudinally restricted and warm temperate palaeobotanical province stretched from Timor, through northwestern Australia, India, easternmost Antarctica, northern Madagascar and east Africa to northwestern Argentina (Peyrot *et al.*, 2019; Césari & Colombi 2013; Kustatscher *et al.* 2018). It differs from the more southerly Ipswich Microflora (Dolby & Balme 1976) by its greater diversity of gymnosperms and the presence of distinctive Eurasian palynofloral components, such as *Camerosporites, Enzonalasporites, Ephedripites* (Fig. 5A), *Infernopollenites, Minutosaccus* (Fig. 5B), *Ovalipollis, Rimaesporites, Samaropollenites* (Fig. 5C) and *Aulisporites* (Fig. 5D). In Western Australia, these assemblages are well documented from the Bonaparte, Browse, Northern Carnarvon and Roebuck basins (Dolby & Balme 1976; Helby *et al.* 1987; Backhouse & Balme 2002; and many unpublished industry reports) and peaked in diversity during the Carnian and Norian (Late Triassic). The Ipswich Microflora is representative of low-diversity, cool temperate, *Dicroidium/Falcisporites*-dominated assemblages in eastern and southern Australia. This palaeobotanical province also ranged across much of Antarctica, southern Africa, Argentina and the Perth Basin in Western Australia where drier conditions persisted for longer than in the northern half of the state. These Middle–Late Triassic palynofloras prevailed without significant change until the end of that period.

JURASSIC–EARLY CRETACEOUS: THE INITIATION OF MODERN VEGETATION

The Triassic–Jurassic boundary marks one of the 'big five' global extinction events (Hull & Darroch 2013). In Western Australia, it is usually manifest by the reduced frequency of *Falcisporites* (collapse of the *Dicroidium* flora) followed by an abundance of *Classopollis* in low-diversity assemblages. This substantial floristic modification, as implied by the distinctive changes in the palynological assemblages, was probably triggered by drastic and rapid palaeoenvironmental changes. The Jurassic and Early Cretaceous palynology of Western Australia has been documented by Balme (1957, 1964), Filatoff (1975), Helby *et al.* (1987) and Backhouse (1978, 1988). Detailed studies of the Cattamarra Coal Measures (formerly a member of the now-superseded Cockleshell Gully Formation), and the succeeding Cadda and Yarragadee formations in the Perth Basin reveal relatively diverse assemblages with abundant conifer pollen attributed to the taxodioid members of Cupresaceae (bald-cypress/redwood family) and Cheirolepidiaceae. The latter represents a group of extinct conifers traditionally associated with arid or saline coastal environments (Alvin 1982); however, in some regions, they also extended into seasonally humid settings (McLoughlin *et al.* 2002; Tosolini *et al.* 2015). Cheirolepid conifers produced the distinctive

Classopollis (aka *Corollina*) pollen (Figs 5E, F). The Early Jurassic was also characterised by increasing abundance of pollen attributable to Araucariaceae (family of the extant Bunya and Norfolk pines). This circumstance, together with a proliferation of fern spores from families with extant representatives, established floral elements characteristic of modern Australia and elsewhere in the southern hemisphere. The proportion of Araucariaceae pollen, particularly *Callialasporites turbatus* (Fig. 5G), increased toward the end of the Early Jurassic. Other araucarian pollen, such as *C. dampieri* (Fig. 5H) and *Araucariacites australis* (Fig. 5I), also became common and increased in abundance through the Late Jurassic. Spores of the modern fern families Anemiaceae (Figs 5J, K), Gleicheniaceae (Fig. 5L), Cyatheaceae (Fig. 5M) and Osmundaceae (Fig. 5N) represent a conspicuous part of increasingly diverse (c. 100 species) assemblages. Western Australian Early Cretaceous palynofloras, as exemplified by assemblages from the Parmelia Group (Perth Basin), contain a higher proportion of spores compared to those from Jurassic strata (Backhouse 1988). The same families of ferns are represented and lycopod spores, such as *Staplinisporites caminus* (Fig. 5P), *Foveosporites subtriangularis* (Fig. 5Q), *Retitriletes circolumenus* (Figs 5R, S) and *R. clavatoides* (Fig. 5T), increased in abundance. Early Cretaceous palynofloras include lower proportions of conifer pollen, with Araucariaceae comprising 10–30% of the assemblages. Conversely, pollen of Podocarpaceae (e.g. plum pines), including *Microcachryidites antarcticus* (Fig. 5O), became better represented. The inception of monocolpate pollen attributed to flowering plants has not been precisely documented in Western Australia. However, their first appearance during the Barremian–Aptian (Early Cretaceous) is probable considering palynological records from eastern Australia (viz. Eromanga and Gippsland basins; Dettmann 1986; Burger 1990).

Jurassic and Cretaceous megafloras have been described from the Perth, Carnarvon and Canning basins. The review by McLoughlin & Pott (2009) of plant material from the Lower Jurassic Cattamarra Coal Measures and Upper Jurassic Yarragadee Formation of the Perth Basin, and the Dingo Claystone of the Northern Carnarvon Basin, revealed assemblages with subordinate ferns (Fig. 6B), abundant conifers (Figs 6C, E) and bennettitaleans (Figs 6D, F). The latter are extinct seed plants that bore cycad-like fronds, but with distinctive flower-like reproductive structures. Based on detailed analysis and comparison with other coeval Gondwanan floras, McLoughlin & Pott (2009) identified a mesothermal climatic signal. Moreover, some of these plants preserve the scars of feeding and egg-laying insects (Figs 6D, F), thereby providing some of the earliest evidence of plant–arthropod interactions in the Western Australian fossil record (McLoughlin *et al.* 2015). Lower Cretaceous megafloras from the Leederville and Bullsbrook formations (Perth Basin), the Birdrong Sandstone and Nanutarra Formation (Northern Carnarvon Basin) and the Broome Sandstone and Callawa Formation (Canning Basin) have been documented by McLoughlin & Guppy (1993), McLoughlin *et al.* (1995), McLoughlin (1996) and McLoughlin & McNamara (2001). These megafloras contain many taxa in common including conifers, Bennettitales (Figs 6J, M), Pentoxylales (Fig. 6K), umkomasialean seed ferns (Fig. 6O), the lycophytes
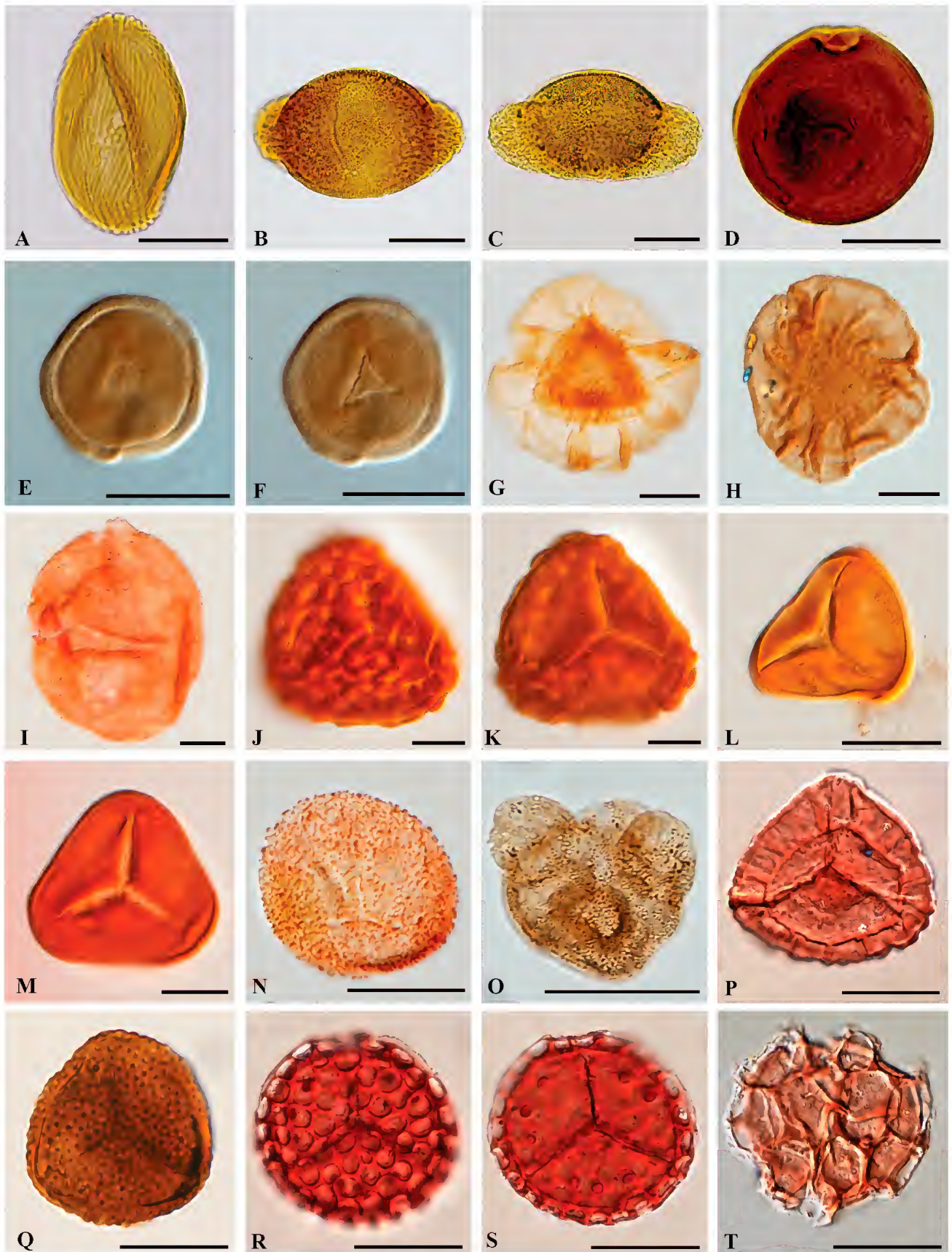
Figure 5. Representative Mesozoic spores and pollen from Western Australia: A *Ephedripites macistriatus*; B *Minutosaccus crenulatus*; C *Samaropollenites speciosus*; D *Aulisporites astigmosus*; E, F *Classopollis* sp., distal and proximal foci; G *Callialasporites turbatus*; H *Callialasporites dampieri*; I *Araucariacites australis*; J, K *Ischyosporites marburgensis*, distal and proximal foci; L *Matonisporites crassiangulatus*; M *Cyathidites minor*; N *Osmundacidites welmanii*; O *Microcachryidites antarcticus*; P *Staplinisporites caminus*; Q *Foveosporites subtriangularis*; R, S *Retitriletes circolumenus*, distal and proximal foci; T *Retitriletes clavatoides*. Scale bars: 20 μm. Ages: A–S, Triassic; E–N, Jurassic; O–T, Early Cretaceous. See appendices for additional information.
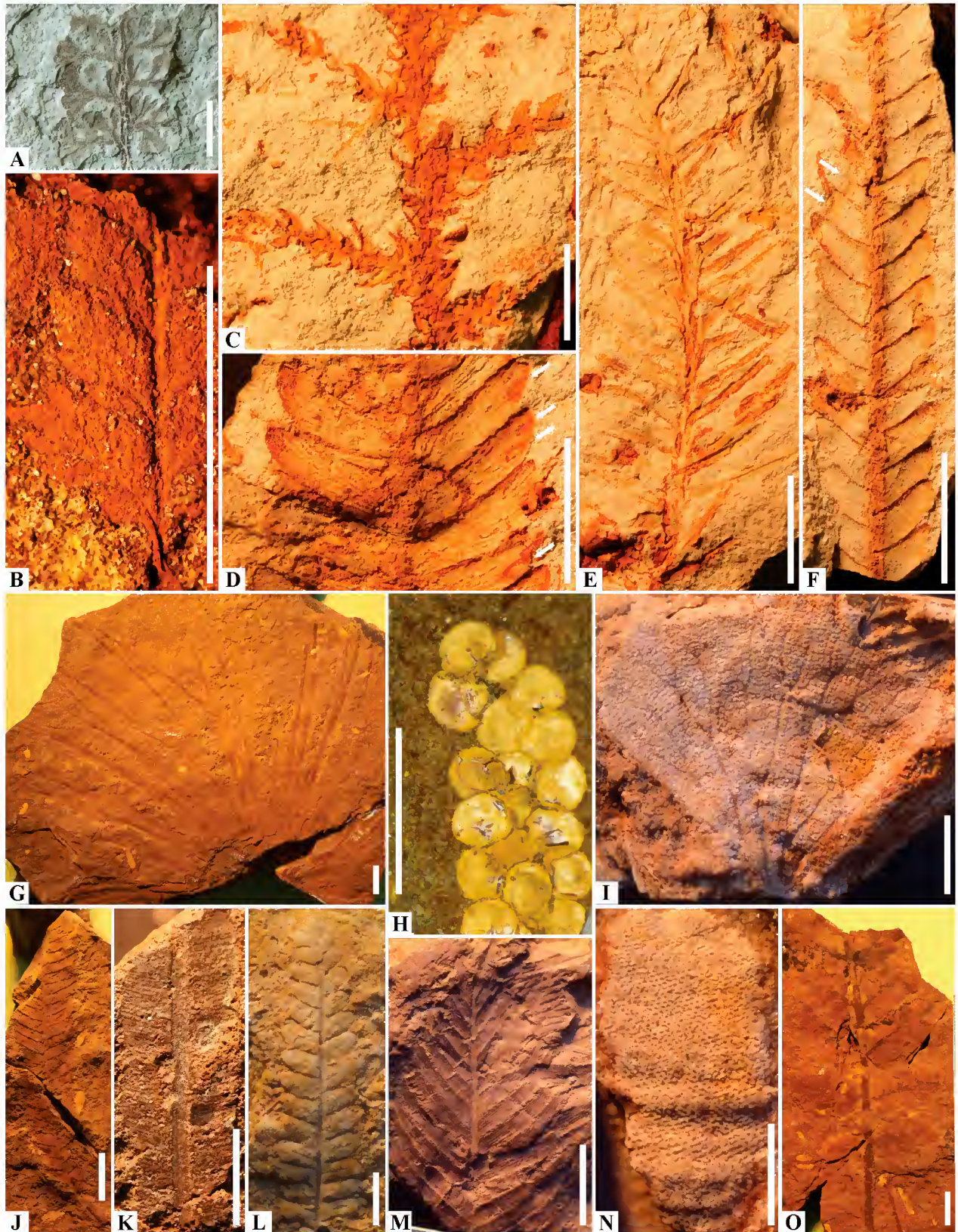
Figure 6. Representative Mesozoic plant megafossils from Western Australia: A cf. *Nymboidiantum multilobatum* (diminutive fern pinna); B *Sphenopteris* sp. (fern pinna), AMF58770; C *Pagiophyllum amanguanus* (conifer shoot with awl-shaped leaves), AMF53736; D *Otozamites linearis* (central portion of a bennettitalean leaf with arrow indicating insect oviposition scars on pinnules), AMF-58731B; E *Elatocladus confertus* (planated coniferous short shoot), AMF-58726; F *Ptilophyllum cutchense* (bennettitalean leaf with arrow indicating insect feeding damage to pinnule apices), AMF-58756; G *Isoetites elegans* (tuft of isoetalean microphylls), UWA-16687; H Cluster of megaspores associated with *Isoetites elegans*, UWA-16687; I *Hausmannia* sp. (dipteridacean fern frond), WAM-P.88.13; J *Ptilophyllum cutchense* (bennettitalean leaf), UWA-16684; K *Taeniopteris daintreei* (pentoxylalean leaf), AMF-58781; L *Cladophlebis* sp. cf. *C. oblonga* (osmundaceous fern pinna), WAM-P.88.12; M *Ptilophyllum acutifolium* (bennettitalean leaf), WAM-P.96.2; N *Nathorstianella babbagensis* (isoetalean corm impression with spirally arranged leaf/root scars), WAM-P.88.2; O *Komlopteris* sp. cf. *K. indica* (seed fern leaf), UWA-16690. Scale bars: 10 mm, except for A: 2 mm, and H: 1 mm. Ages: A, Early Triassic; B–F, Early Jurassic; G–O, Early Cretaceous. See appendices for additional information.

Nathorstianella babbagensis (Fig. 6N) and *Isoetites elegans* (Figs 6G, H), and diverse ferns attributed to the families Dipteridaceae (Fig. 6I), Osmundaceae (Fig. 6L) and Gleicheniaceae.

Late Cretaceous – Holocene: development of flowering plants

During the Cretaceous and early Cenozoic, global vegetation changed from mostly gymnosperms and ferns to predominantly angiosperms (flowering plants). The best known, reasonably well-dated, Late Cretaceous – Holocene floras in Western Australia are from the South West, a region now recognised as a biodiversity hotspot of global significance. In contrast to southeastern Australia, where some fossil palynofloras (pollen and spore assemblages) are well-known from continuous sedimentary successions, palynological studies in Western Australia have been limited, in part due to stratigraphic and geographic discontinuity. For this reason, many studies in the state document spore-pollen assemblages from a single palynozone, and substantial chronostratigraphic intervals are under-represented in the sedimentary record. For example, late Eocene plant megafossils and palynomorphs are well represented, whereas those from the early Eocene and late Oligocene are either absent or incompletely known.

Previous accounts of plant fossils, geology and climates through time in Western Australia (McLoughlin & Hill 1996; McLoughlin & McNamara 2001; Dodson *et al.* 2000; Dodson *et al.* 2002) are updated here to incorporate more recent research. The focus herein is on the mid-Late Cretaceous, the late Eocene and the Pliocene–Holocene for reasons mentioned above.

MID-LATE CRETACEOUS (~83 Ma): RISE OF THE PROTEACEAE

In contrast to dinoflagellate cyst assemblages (Backhouse 2006), spore-pollen successions from the early Late Cretaceous (Cenomanian–Coniacian) of Western Australia have yet to be thoroughly documented. Available data suggest that non-magnoliid angiosperms were not introduced into Western Australian vegetation until the Cenomanian (Balme 1964). This contrasts with the records documented in southern Victoria (Dettmann 1986; Korasidis *et al.* 2016), Queensland (Dettmann 1973; Burger 1993) and Antarctica (Dettmann & Thomson 1987) that indicate the presence of this group in lower Albian (upper Lower Cretaceous) strata. Dettmann's (2017) regional study envisaged widespread Albian – early Late Cretaceous forests and woodlands dominated by Araucariaceae, Cheirolepidiaceae and Podocarpaceae with ground communities comprising ferns, lycopods and bryophytes. These conifer-dominated forests may have produced amber (Quinney *et al.* 2015) as in coeval northern hemisphere temperate forests (Barron *et al.* 2015; Peyrot *et al.* 2019).

Palynofloras are rare in mid-Upper Cretaceous (Santonian – lower Campanian) strata of the southern and central Perth Basin (Milne 2018). Numerous conifers, ferns and mosses probably grew in marshy areas near or adjacent to highly diverse communities dominated by Proteaceae (family of *Banksia* and *Grevillea*). Pollen of other flowering plants are still infrequent. The presence of charcoal indicates that the vegetation was burnt regularly. Overall, it is likely that the Perth Basin vegetation was similar to that reported from later in the Cretaceous by Carpenter *et al.* (2015, 2016); i.e., expanses of heathy vegetation with abundant Proteaceae, gymnosperms and palms, perhaps interspersed among pockets of more closed forest types with early representatives of Antarctic Beech (*Nothofagus*).

Although many of the Cretaceous proteaceous pollen types probably belong to extinct lineages, some of which continued into the early Cenozoic, several distinctive species bear striking resemblances to pollen of modern plants in Western Australia. Remarkably, *Proteacidites palisadus* (Figs 7E, F) shares important features with *Franklandia* pollen (Martin 1995; Sauquet *et al.* 2009); the two species of that genus are now found only in the state's South West. Other distinctive *Proteacidites* species include *P. annularis*, *P. adenanthoides* and *P. concretus*. *P. annularis* (Fig. 7G) is similar to pollen of *Xylomelum* (Woody Pear) and particularly to *X. occidentale*, the southernmost of the two Western Australian species (Milne 1994). *Proteacidites adenanthoides* (Fig. 7H) is akin to pollen from *Adenanthos* (Cookson 1950), a genus with its centre of diversity in the South West. *Proteacidites concretus* resembles pollen of *Macadamia* and *Helicia* (Dettmann & Jarzen 1996), genera that are native to eastern Australian rainforests. Common spores include *Cyathidites* spp., which are similar to spores produced by extant fern families Cyatheaceae and Dicksoniaceae (tree ferns), and *Clavifera triplex* (Fig. 7I), referable to Gleicheniaceae, which are now confined to northernmost regions of the state. Conifer pollen include *Phyllocladidites mawsonii* (Fig 7J) and *Lygistepollenites florinii* (Fig 7K), similar to that now produced by the Tasmanian Huon Pine and the New Zealand Rimu, respectively.

LATE EOCENE (~40 Ma): RAINFORESTS AND HEATHLANDS CO-EXIST

Near the close of the Cretaceous, southern Western Australia was at similar latitudes to the present Antarctic coast, but a gulf then opened from the west to the Tasmanian region, with the final separation of the two continents at about 40 Ma. It is argued that climates in southern Australia during parts of the early Eocene were extremely warm (Carpenter *et al.* 2012), as elsewhere, partly due to high levels of carbon dioxide. The climate of southwestern Australia was also influenced by the combination of a shallow, sluggish, clockwise current within this gulf and warm Indian Ocean water from the tropics (Exon *et al.* 2004). The northward drifting of Australia and South America away from Antarctica resulted in the formation of a fully circumpolar ocean current and, consequently, a shift to a markedly cooler climate around the end of the Eocene.

Extensive palaeodrainage systems, such as those emptying into the vast Eucla Basin, point to overall much wetter climates in the Eocene than today (Clarke *et al.* 2003). However, pluvial climates do not necessarily produce densely rain-forested landscapes, especially
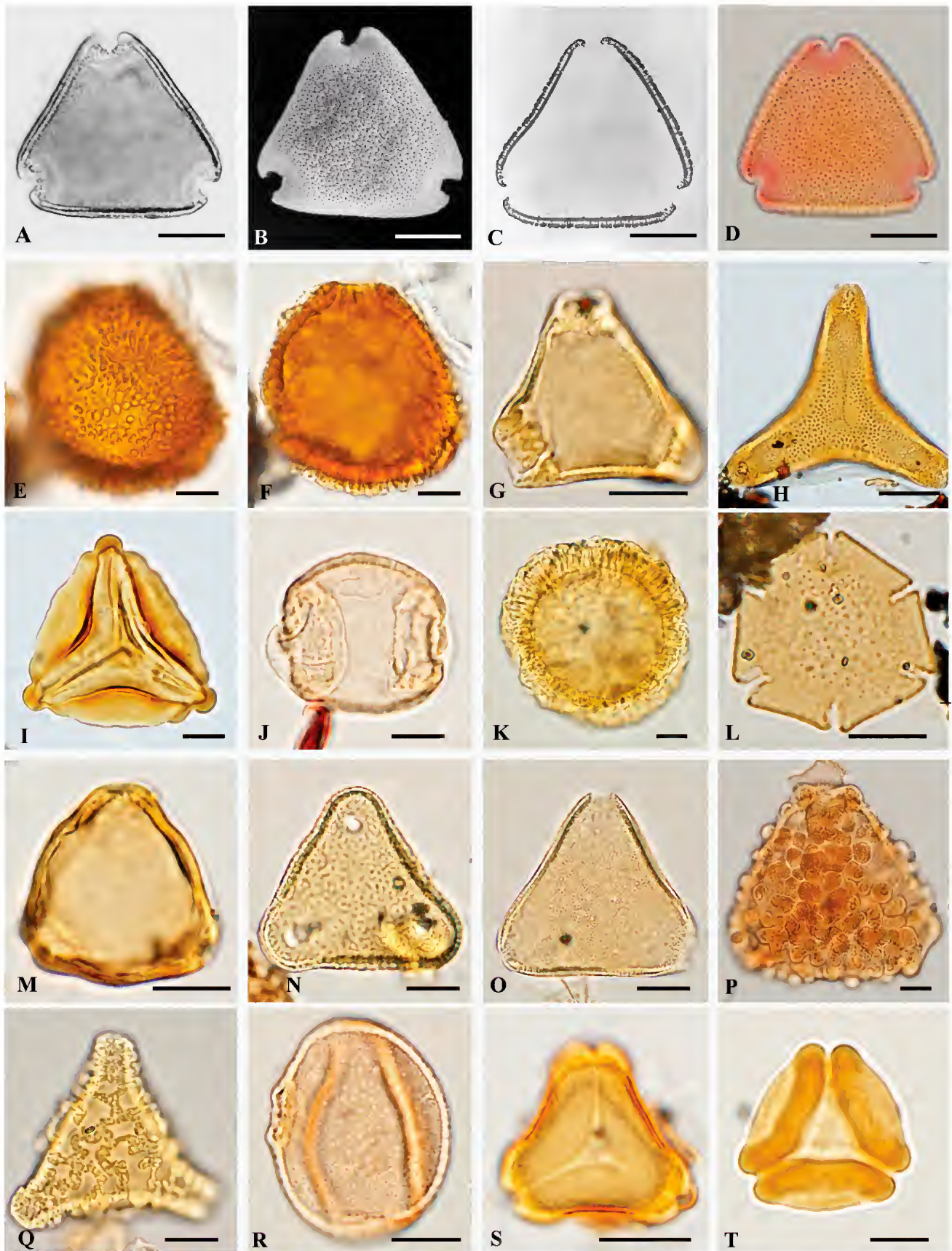
Figure 7. Representative Late Cretaceous and Cenozoic pollen from Western Australia: A–D *Proteacidites carobelindiae* (A medial focus TLM, B same specimen in SEM, C same specimen in TEM, D high focus); E, F *Proteacidites palisadus*, proximal and medial foci; G *Proteacidites annularis*; H *Proteacidites adenanthoides*; I *Clavifera triplex*; J *Phyllocladidites mawsonii*; K *Lygistepollenites florinii*; L *Nothofagidites* cf. *emarcidus*; M *Haloragacidites harrisii*; N *Anacolosidites acutullus*; O *Proteacidites punctiporus*; P *Proteacidites cumulus*; Q *Proteacidites reticulatus*; R *Milfordia homeopunctata*; S *Myrtaceidites eucalyptoides*; T *Eucalyptus marginata*. Scale bars: 10 μm. Ages: A–D, G, J, K, N–R, late Eocene; E, F, late Paleocene; H, I, Late Cretaceous; L, M, S, Miocene – early Pliocene; T, Holocene. See appendices for additional information.

when considering the extremely ancient and nutritionally poor nature of most Western Australian soils.

Late Eocene palynofloras include those described from the Bremer Basin (Stover & Partridge 1982), Zanthus on the western margin of the Eucla Basin (Milne 1988), Lake Lefroy near Kambalda (Itzstein-Davey 2004), the Muir–Unicup catchment near Manjimup (Al-Shawareb 2009) and Mulga Rock just north of the Eucla Basin (Mack & Milne 2015). Moss and fern spores are minor components of these assemblages. Conversely, pollen from wind-pollinated plants are abundant and include Araucariaceae; *Nothofagidites* spp. (Fig. 7L; related to the Southern Beech *Nothofagus*); and *Haloragacidites harrisii* (Fig. 7M) that embraces a range of Casuarinaceae species (she-oaks). Myrtaceae pollen, including that of *Eucalyptus* and *Melaleuca*, have been recorded in varying proportions in upper Eocene successions, being more common in the Mulga Rock assemblages than at Zanthus (Milne 1988; Mack & Milne 2015).

The late Eocene palynofloras include elements suggesting affinities with modern vegetation types characterising southern hemisphere high-latitude, temperate regions and high-altitude cool tropical regions. The rare presence of pollen assigned to *Anacolosidites acutullus* (Fig. 7N) and *Beaupreaidites elegansiformis* reflects the integration of tropical plants related to *Anacolosa* (Cookson & Pike 1954; Macphail 1999) and *Beauprea spathulaefolia* (Cookson 1950; Milne 1998b), the former of which is now confined in Australia to northern Cape York Peninsula in Queensland, and the latter is endemic to New Caledonia. These palynofloras also contain small numbers of presumably animal/insect pollinated proteaceous pollen types including *Banksieaeidites*, which have been related to modern Musgraveinae of the Queensland wet tropics and to *Banksia*; and *Proteacidites carobelindiae* (Figs 7A–D) and *P. cirritulus*, related to *Petrophile* (Mack & Milne 2015, 2016; Milne 1998b; Milne & Martin 1998). Other consistently recorded Proteaceae include *Proteacidites punctiporus* (Fig. 7O), *P. cumulus* (Fig. 7P) and *P. reticulatus* (Fig. 7Q). Collectively, these pollen signify the local presence of sclerophyllous plant communities, probably in mosaic with rainforest.

Western Australian late Eocene mega- and mesofossil evidence largely agrees with that from microfossils. Borehole samples have yielded diverse, well-preserved leaf cuticles—the outer resistant layer of a leaf that carries a 'fingerprint' of cellular details including stomata, glands, hairs and regular epidermal cells (Figs 8A, C, D, H, I; Carpenter & Pole 1995; Carpenter *et al.* 2017). The cuticular remains are generally indicative of warm and wet forest vegetation, especially *Gymnostoma* (Casuarinaceae), certain Proteaceae and Lauraceae (avocado and cinnamon family), which have numerous extant species in eastern Australian rainforests. Other fossils include the conifers, such as probable *Agathis* (Araucariaceae; Fig. 8A), *Libocedrus* (Cupressaceae), and the podocarps *Acmopyle*, *Dacrycarpus* (cf. Figs 8B, C) and *Dacrydium* (Fig. 8D). Foliage of *Nothofagus* (cf. Figs 8E, F) is also known, with one leaf species from the Kojonup Sandstone (Scriven *et al.* 1995) being strikingly similar to deciduous forms from South America. A noteworthy recent discovery from this region (by RJC) is that of the cycad *Bowenia* (Figs 8G, H), which is now represented globally by only two species in the Queensland tropics

but was widespread across southern Australia during the late Paleogene (Hill *et al.* 2019).

There are also mega- and mesofossil signals of more open, sclerophyllous vegetation, which probably grew on variably swampy sites that could not support tall, closed rainforest. The apparent importance of Western Australia as a centre of sclerophyll evolution in the late Eocene (or earlier) is probably related to the state having some of the Earth's most impoverished soils (especially in phosphorus). Most notably, an apparent ancient diversification of *Banksia* is expressed in the Western Australian fossil record and may even reflect the strengthening of seasonal climates in the region. In particular, two very different late Eocene fossil *Banksia* leaf types exhibit morphologies that are classical transpiration-limiting adaptations (Hill 1998) of extant open heathland species of the South West. Thus, among the several *Banksia*-like leaf types (Figs 8J, L) in the Kojonup Sandstone is *B. paleocrypta* (Fig. 8L), which is remarkably similar to the extant *B. menziesii* (Fig. 8M) and *B. burdettii*, and features pronounced lower surface crypts with enclosed stomata (Carpenter *et al.* 2014). Another leaf type from the Zanthus lignite, *B.* sp. nov., is extremely small (< 1.5 mm wide) with leaf margins that are rolled under to almost meet at the lower midvein, a form shown by several extant South West species, including *B. nutans* and *B. tricuspis* (Carpenter & Milne in press). There is at least one other striking example of late Eocene mesofossils of Proteaceae that belong to a group well-represented in modern heathlands of the state's South West: Carpenter *et al.* (2017) documented the presence of cuticles (Fig. 8I) that are very similar to those of the snotty gobbles (*Persoonia* spp.). The Eocene–Oligocene plant assemblage preserved in lateritised strata at West Dale, southwestern Australia, represents another example of a megaflora incorporating diverse Proteaceae and Myrtaceae of sclerophyllous aspect (Hill & Merrifield 1993) associated with taxa more typical of rainforests (e.g. *Nothofagus, Gymnostoma, Agathis, Dacrycarpus* and *Retrophyllum*). The co-occurrence of mesomorphic and sclerophyllous leaf types at West Dale supports the existence of locally mixed communities incorporating some plants with high water requirements and others tolerant to water stress. It is likely that some of these plants, which evolved sclerophylly as an adaptation initially to growth on low-nutrient substrates, were pre-adapted to coping with drought as the Western Australian landscape became progressively drier following the Eocene.

PLIOCENE–HOLOCENE: A LANDSCAPE SHAPED BY HIGHLY VARIABLE CLIMATES

Palynological studies of Neogene sediments in Western Australia are widely spread from the South West (Bint 1981) to offshore northwest (Martin & McMinn 1994); in the Yallalie Crater, c. 200 km north of Perth (Atahan *et al.* 2004; Dodson & Macphail 2004); and on the Nullarbor Plain on the state's south-easternmost border (Sniderman *et al.* 2016). All these deposits have been dated as Pliocene, but Macphail (1997) suggested that the lower part of Bint's (1981) Lake Tay deposit could be as old as late Miocene.
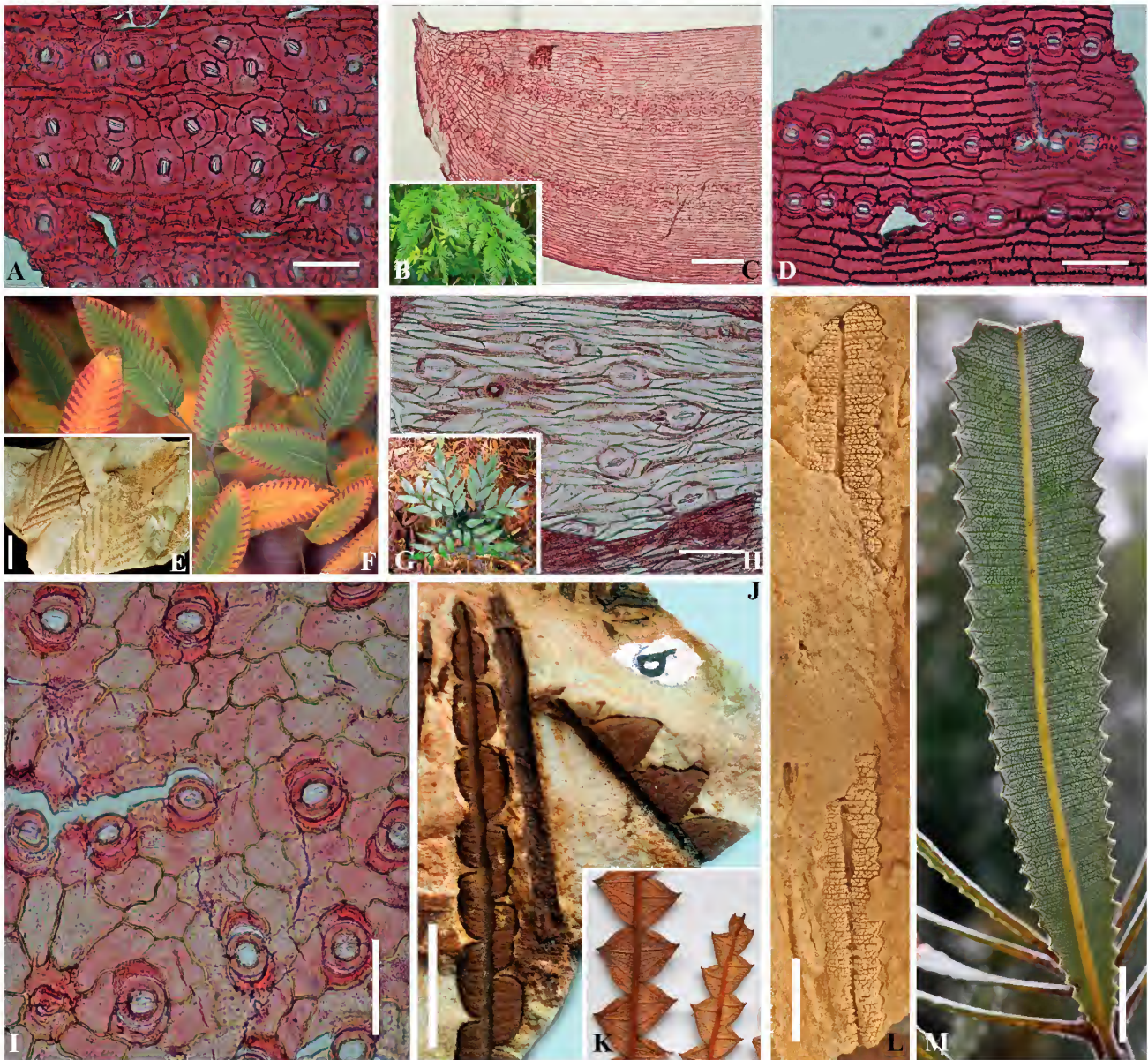
Figure 8. Representative Cenozoic plant mega- and mesofossils from Western Australia, and examples of extant relatives: A cuticle of Araucariaceae, probably *Agathis*; B extant *Dacrycarpus vieillardii* foliage; C apex of *Dacrycarpus* leaf; D cuticle of *Dacrydium*; E *Nothofagus plicata*; F extant *Nothofagus alpina*; G extant *Bowenia spectabilis*; H cuticle of *Bowenia*; I cuticle of Persoonieae; J *Banksia*-like foliage, UWA-118109; K extant *B. candolleana*, AQ333988; L *B. paleocrypta*, WAM; M extant *B. menziesii*. Scale bars: A, D, H, I 100 µm, C 200 µm, E, J, L 10 mm. Ages: A, C–E, H–J, L, Cenozoic; B, F, G, K, M, modern. See appendices for additional information.

A long-term trend of post-Eocene cooling and aridification is well recognised in Australia, but palynofloral evidence shows that, during the Pliocene, freshwater habitats and wet-forest plants were much more widespread than in present-day Western Australia. Sniderman *et al.* (2016) interpreted a warm/wet climatic interval within the early Pliocene on the basis of pollen assemblages from caves in the Nullarbor Plain. These authors showed that, soon after 5 Ma, in the early Pliocene, sparse shrub- or woodlands reflecting semi-aridity gave way to wetter eucalypt forests with understorey plants, including a type of *Banksia* and the spear-lily *Doryanthes*, that are now confined to coastal eastern Australia.

This relatively benign climate lasted for ~1.5 Ma (Sniderman *et al.* 2016), but mesic-adapted lineages appear to have persisted much longer, at least north of Perth. Important evidence for this comes from mid-Pliocene lake sediments within the Cretaceous 12-km-wide Yallalie asteroid impact crater (Atahan *et al.* 2004; Dodson & Macphail 2004). These sediments contain pollen of sclerophyll forest, heathland and semi-arid plant groups still present in southwestern Australia, along with other plants now confined to Australasian temperate and subtropical–tropical rainforests. The vegetation seems to have undergone repeated pronounced changes, probably in response to significant climatic fluctuations.

Despite climate variability, the overall palynological trends from the late Miocene to the Holocene show a decrease in Casuarinaceae pollen and a concomitant increase in Myrtaceae pollen (Fig. 7S), grasses, Chenopodiaceae (saltbushes) and daisies, whereas Restionaceae (Fig. 7R) abundances fluctuate. Most of the Pliocene assemblages include pollen of plants similar to extant species alongside a few wetter forest elements, such as *Araucaria, Agathis, Dacrycarpus, Dacrydium, Nothofagus* and ferns that were present as far back as the late Eocene. In contrast to Eocene sediments, even those with fossils of sclerophyllous vegetation, widespread evidence of frequent burning is apparent from the abundant charcoal observed in the Yallalie crater-fill (Dodson & Macphail 2004) and other upper Cenozoic deposits.

During the Pleistocene (~2.6 Ma to 11 700 years ago) there were even more extreme arid intervals with higher fire frequencies and successive prolonged glacial episodes (ice ages), characterising ~90% of this interval, separated by short, warm inter-glacials. These conditions likely contributed to the final demise of the remnant wetter forest elements in southwestern Australia. Nevertheless, frog fossils from the Nullarbor Plain indicate that at least seasonally moist conditions prevailed there in the early Pleistocene (Tyler & Prideaux 2016). This concurs with palynofloral evidence that the modern dominance of arid-adapted grasslands and shrublands, with chenopods and daisies, probably commenced in the middle Pleistocene (Sniderman *et al.* 2016).

During the last glacial maximum (global LGM: 21±3 ka) of the late Pleistocene, only a small region of Tasmania and southeastern Australia was glaciated (Barrows *et al.* 2002). However, very cold climatic conditions appear to have led to the demise of the eucalypt forests of the now wettest forested regions of the South West and were replaced by shrublands during an interval of perhaps 10 000 years (Sniderman *et al.* 2019).

The Holocene—the most recent epoch in Earth history—spans the last c. 11 700 years. Holocene palynofloras of the South West differ regionally, as does the vegetation of southern Western Australia today. For example, mid-Holocene palynological assemblages from Walpole (west of Albany) are dominated by eucalypt pollen (Churchill 1968; Newsome & Pickett 1993), whereas Casuarinaceae are the more prominent elements of the contemporary palynoflora of Two Mile Lake, south of the Stirling Ranges (Itzstein-Davey 2004). Palynofloras from peat near Manjimup indicate communities containing Casuarinaceae and eucalypts, with a heath understorey, in the early Holocene; and in the middle Holocene, alternating dominance of *Corymbia calophylla* (Marri) and *Eucalyptus marginata* (Jarrah, Fig. 7T) forests, with *Melaleuca* woodlands in wetland areas (Dodson & Lu 2000). The mid- to late Holocene palynofloras from Barker Swamp, Rottnest Island, suggest widespread *Callitris* (Rottnest Island Pine) forest with sedges (Cyperaceae) growing in the immediate vicinity, together with woodland incorporating tuart (*Eucalyptus gomphocephala*) and jarrah (Backhouse 1993). Late Holocene charcoal laminae in Barker Swamp are followed by a decline in *Callitris*, reflecting changes to a more open vegetation dominated by Asteraceae (daisies).

Newsome & Pickett (1992), Dodson & Lu (2000) and Itzstein-Davey (2004) concur that the mid- to late Holocene in southwestern Australia appears to have experienced relative climatic stability and that the vegetation was not unlike that of today. Fluctuations in pollen assemblages of lake and swamp sediments were evidently due more to local environmental changes (e.g. burning patterns, other species interactions, facies changes) than to major climatic changes.

SUMMARY AND CONCLUSIONS

This review of broad trends in Western Australian plant communities and landscape evolution over the past 470 Ma (summarised in Fig. 9) is underpinned by substantial palaeobotanical and palynological data published since 1960. The earliest terrestrial Western Australian plant communities are Middle Ordovician based on palaeontological data, including palynological and molecular records, from the Canning Basin. Ordovician–Devonian palynological data are mainly from the Canning Basin. Late Devonian arborescent communities were widespread across the state. The Mississippian flora is inferred almost exclusively from palynological data sourced from the Canning, Carnarvon and Perth basins.

The oldest known pollen are dated as late Serpukhovian (latest Mississippian) indicating the colonisation of drylands by gymnosperms. The scarce record for the Pennsylvanian reflects a major cooling episode, resulting in the establishment of an extensive ice sheet covering the state. The Permian flora, developed in the aftermath of the preceeding ice age, is particularly well represented by palyno- and megafloral assemblages, both signifying the prevalence of swampy lowland plant communities dominated by arborescent *Glossopteris*.

The megafloral and palynological evidence from the Early–Middle Triassic indicates a distinctive, low-diversity flora comprising mainly herbaceous lycopsids, ferns and other low-stature plants replaced eventually by seed ferns typified by *Dicroidium*. The major turnover in Western Australia's vegetation during the Triassic–Jurassic transition is reflected by the replacement of *Falcisporites* (produced by *Dicroidium*) by *Classopollis* (Cheirolepidaceae), the latter becoming dominant in palynological assemblages. Upper Jurassic – Lower Cretaceous successions provide a rich and diverse megafloral and palynological record documenting the evolution and radiation of conifer and fern families with extant representatives. The colonisation of the landscape by flowering plants during the Barremian–Albian (late Early Cretaceous) remains poorly constrained temporally. Palynological successions of the Perth Basin indicate that Proteaceae were probably significant components of the Campanian vegetation.

Palynological and palaeobotanical evidence points to the presence of mixed floral communities (rainforests and sclerophyllous vegetation) during the Eocene. Palynological data from the Pliocene indicate short-lived resurgences of wetter conditions and associated expansion of wet forests within the long-term Neogene cooling and aridification of the Western Australian climate. In the middle Pleistocene, arid-adapted,
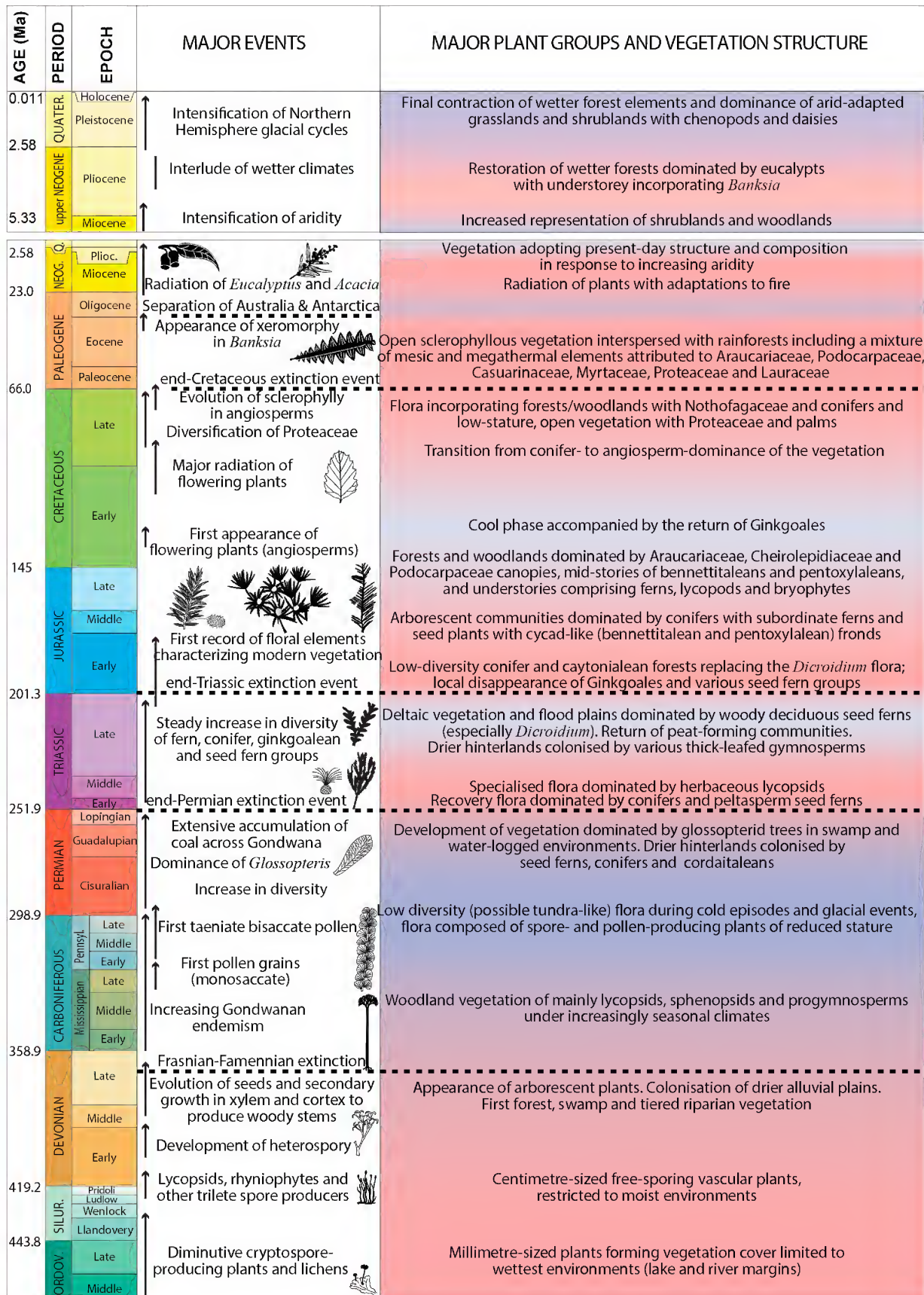
AGE (Ma)	PERIOD	EPOCH	MAJOR EVENTS	MAJOR PLANT GROUPS AND VEGETATION STRUCTURE
0.011	QUATER.	Holocene/ Pleistocene	Intensification of Northern Hemisphere glacial cycles	Final contraction of wetter forest elements and dominance of arid-adapted grasslands and shrublands with chenopods and daisies
2.58	upper NEOGENE	Pliocene	Interlude of wetter climates	Restoration of wetter forests dominated by eucalypts with understorey incorporating *Banksia*
5.33		Miocene	Intensification of aridity	Increased representation of shrublands and woodlands
2.58	NEOG. Q.	Plioc. Miocene	Radiation of *Eucalyptus* and *Acacia*	Vegetation adopting present-day structure and composition in response to increasing aridity. Radiation of plants with adaptations to fire
23.0	PALEOGENE	Oligocene	Separation of Australia & Antarctica. Appearance of xeromorphy in *Banksia*	
		Eocene		Open sclerophyllous vegetation interspersed with rainforests including a mixture of mesic and megathermal elements attributed to Araucariaceae, Podocarpaceae, Casuarinaceae, Myrtaceae, Proteaceae and Lauraceae
66.0		Paleocene	end-Cretaceous extinction event	
	CRETACEOUS	Late	Evolution of sclerophylly in angiosperms. Diversification of Proteaceae	Flora incorporating forests/woodlands with Nothofagaceae and conifers and low-stature, open vegetation with Proteaceae and palms. Transition from conifer- to angiosperm-dominance of the vegetation
			Major radiation of flowering plants	
145		Early	First appearance of flowering plants (angiosperms)	Cool phase accompanied by the return of Ginkgoales
	JURASSIC	Late Middle		Forests and woodlands dominated by Araucariaceae, Cheirolepidiaceae and Podocarpaceae canopies, mid-stories of bennettitaleans and pentoxylaleans, and understories comprising ferns, lycopods and bryophytes
		Early	First record of floral elements characterizing modern vegetation. end-Triassic extinction event	Arborescent communities dominated by conifers with subordinate ferns and seed plants with cycad-like (bennettitalean and pentoxylalean) fronds. Low-diversity conifer and caytonialean forests replacing the *Dicroidium* flora; local disappearance of Ginkgoales and various seed fern groups
201.3	TRIASSIC	Late	Steady increase in diversity of fern, conifer, ginkgoalean and seed fern groups	Deltaic vegetation and flood plains dominated by woody deciduous seed ferns (especially *Dicroidium*). Return of peat-forming communities. Drier hinterlands colonised by various thick-leafed gymnosperms
		Middle Early	end-Permian extinction event	Specialised flora dominated by herbaceous lycopsids. Recovery flora dominated by conifers and peltasperm seed ferns
251.9	PERMIAN	Lopingian Guadalupian	Extensive accumulation of coal across Gondwana. Dominance of *Glossopteris*	Development of vegetation dominated by glossopterid trees in swamp and water-logged environments. Drier hinterlands colonised by seed ferns, conifers and cordaitaleans
		Cisuralian	Increase in diversity	
298.9	CARBONIFEROUS	Pennsyl. Late Middle Early	First taeniate bisaccate pollen	Low diversity (possible tundra-like) flora during cold episodes and glacial events, flora composed of spore- and pollen-producing plants of reduced stature
		Mississippian Late	First pollen grains (monosaccate)	
		Middle	Increasing Gondwanan endemism	Woodland vegetation of mainly lycopsids, sphenopsids and progymnosperms under increasingly seasonal climates
358.9		Early	Frasnian-Famennian extinction	
	DEVONIAN	Late	Evolution of seeds and secondary growth in xylem and cortex to produce woody stems	Appearance of arborescent plants. Colonisation of drier alluvial plains. First forest, swamp and tiered riparian vegetation
		Middle	Development of heterospory	
		Early		
419.2	SILUR.	Pridoli Ludlow Wenlock	Lycopsids, rhyniophytes and other trilete spore producers	Centimetre-sized free-sporing vascular plants, restricted to moist environments
		Llandovery		
443.8	ORDOV.	Late Middle	Diminutive cryptospore-producing plants and lichens	Millimetre-sized plants forming vegetation cover limited to wettest environments (lake and river margins)

Figure 9. Major plant-evolutionary events and vegetation changes in Western Australia. The blue and red backgrounds represent cooler and warmer episodes, respectively.

fire-tolerant grasslands and shrublands replaced the last stands of mesothermal forests dominated by Araucariaceae, Podocarpaceae and Nothofagaceae. In the mid-late Holocene, the vegetation of the South West developed into that which we know today: a mosaic of sclerophyll forests and woodlands, heath and wetlands.

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REFERENCES

Al-Shawareb A 2009. Eocene palynology of a lignite section in the Muir-Unicup Catchment, Werillup Formation, south Western Australia. *BSc Honours Thesis, University of Western Australia*, 98 p. (unpublished).

Algeo T J & Twitchett R J 2010. Anomalous Early Triassic sediment fluxes due to elevated weathering rates and their biological consequences. *Geology* 38, 1023–1026.

Alvin K L 1982. Cheirolepidiaceae: Biology, structure and paleoecology. *Review of Palaeobotany and Palynology* 37, 71–98.

Apak S N & Backhouse J 1998. Stratigraphy and petroleum exploration objectives of the Permian–Carboniferous of the Barbwire Terrace and adjacent areas, northeast Canning Basin. *Geological Survey of Western Australia, Report* 68, 30 p.

Atahan P Dodson JR & Itzstein-Davey F 2004. A fine resolution Pliocene pollen and charcoal record from Yallalie, southwestern Australia. *Journal of Biogeography* 31, 199–205.

Backhouse J 1978. Palynological zonation of the Late Jurassic and Early Cretaceous sediments of the Yarragadee Formation, central Perth Basin, Western Australia. *Geological Survey of Western Australia, Report* 7, 52 p.

Backhouse J 1988. Late Jurassic and Early Cretaceous palynology of the Perth Basin, Western Australia, *Geological Survey of Western Australia, Bulletin* 135, 126 p.

Backhouse J 1991. Permian biostratigraphy of the Collie Basin, Western Australia. *Review of Palaeobotany and Palynology* 67, 237–314.

Backhouse J 1993. Holocene vegetation and climate record from Barker Swamp, Rottnest Island, Western Australia. *Journal of the Royal Society of Western Australia* 76, 53–61.

Backhouse J & Balme B E 2002. Late Triassic palynology of the Northern Carnarvon Basin. *Minerals and Energy Research Institute of Western Australia (MERIWA) Report* 226, 168 p.

Backhouse J 2006. Albian (Lower Cretaceous) dinoflagellate cyst biostratigraphy of the lower Gearle Siltstone, Southern Carnarvon Basin, Western Australia. *Palynology* 30, 43–68.

Balme B E 1957. Spores and pollen grains from the Mesozoic of Western Australia. *Commonwealth Scientific and Industrial Research Organization (Australia), Coal Research Section, Technical Communication* 25, 48 p.

Balme B E 1962. Upper Devonian (Frasnian) spores from the Carnarvon Basin, Western Australia. *The Palaeobotanist* 9, 1–10.

Balme B E 1963. Plant microfossils from the Lower Triassic of Western Australia. *Palaeontology* 6, 12–40.

Balme B E 1964. The palynological record of Australian pre-Tertiary floras. Pages 49–80 *in* Cranwell L M, editor *Ancient Pacific Floras*. University of Hawaii Press, Honolulu.

Balme B E 1988. Miospores from Late Devonian (early Frasnian) strata, Carnarvon Basin, Western Australia. *Palaeontographica Abteilung B* 209, 109–166.

Balme B E 1995. Fossil in situ spores and pollen grains: an annotated catalogue. *Review of Palaeobotany and Palynology* 87, 81–323.

Balme B E & Hassell C W 1962. Upper Devonian spores from the Canning Basin, Western Australia. *Micropaleontology* 8, 1–28.

Balme B E & Hennelly J P F 1955. Bisaccate sporomorphs from Australian Permian coals. *Australian Journal of Botany* 3, 89–98.

Balme B E & Hennelly J P F 1956a. Monolete, monocolpate and alete sporomorphs from Australian Permian sediments. *Australian Journal of Botany* 4, 54–67.

Balme B E & Hennelly J P F 1956b. Trilete sporomorphs from Australian Permian sediments. *Australian Journal of Botany* 4, 240–260.

Balme B E & Foster C B 1996. Triassic. Pages 136–147 *in* Young G C & Laurie J R editors *An Australian Phanerozoic Timescale*. Australian Geological Survey Organisation, Canberra.

Barrón E, Peyrot D, Rodríguez-López J P, Meléndez N, López Del Valle R, Najarro M, Rosales I & Comas-Rengifo M J 2015. Palynology of Aptian and upper Albian (Lower Cretaceous) amber-bearing outcrops of the southern margin of the Basque-Cantabrian Basin (northern Spain). *Cretaceous Research* 52, 292–312.

Barrows T T, Stone J O, Fifield L K & Cresswell R 2002. The timing of the last glacial maximum in Australia. *Quaternary Science Reviews* 21, 159–173.

Bateman R M & DiMichele W A 1994. Heterospory: the most iterative key innovation in the evolution of plants. *Biological Reviews* 69, 345–417.

Batten D J 1999. Extraction techniques – Small palynomorphs. Pages 15–19 *in* Jones T P & Rowe NP, editors, *Fossil Plants and Spores: Modern Techniques*. The Geological Society, London.

Bint A N 1981. An early Pliocene pollen assemblage from Lake Tay, south-western Australia and its phytogeographic implications. *Australian Journal of Botany* 29, 277–291.

Bomfleur B, McLoughlin S & Vajda V 2014. Fossilized nuclei and chromosomes reveal 180 million years of genomic stasis in royal ferns. *Science* 343, 1376–1377.

Burger D 1990. Early Cretaceous angiosperms from Queensland, Australia. *Review of Palaeobotany and Palynology* 65, 153–163.

Burger D 1993. Early and middle Cretaceous angiosperm pollen grains from Australia. *Review of Palaeobotany and Palynology* 78, 183–234.

Carpenter R J & Pole M 1995. Eocene plant fossils from the Lefroy and Cowan Paleodrainages, Western Australia. *Australian Systematic Botany* 8, 1107–1154.

Carpenter R J, Jordan G J, Macphail M K & Hill R S 2012. Near-tropical early Eocene terrestrial temperatures at the Australo-Antarctic margin, western Tasmania. *Geology* 40, 267–270.

Carpenter R J, McLoughlin S, Hill R S, McNamara K J & Jordan G J 2014. Early evidence of xeromorphy in angiosperms: stomatal encryption in a new Eocene species of *Banksia* (Proteaceae) from Western Australia. *American Journal of Botany* 101, 1486–1497.

Haig D W, Martin S K, Mory A, McLoughlin S, Backhouse J, Berrell R, Kear B P, Hall R, Foster C B, Chi G R & Bevan J 2015. Early Triassic (early Olenekian) life in the interior of East Gondwana: mixed marine–terrestrial biota from the Kockatea Shale, Western Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **417**, 511–533.

Haig D W, Foster C B, Howe R W, Mantle D, Backhouse J, Peyrot D & Vitacca J 2018. Fossil protists (algae and testate protozoans) in the marine Phanerozoic of Western Australia: a review through latitudinal change, climate extremes, and breakup of a supercontinent. *Journal of the Royal Society of Western Australia* **101**, 44–67.

Helby R 1970. *A biostratigraphy of the Late Permian and Triassic of the Sydney Basin*. PhD Thesis, University of Sydney, 479 p. (unpublished).

Helby R 1973. Review of Late Permian and Triassic palynology of New South Wales. *Geological Society of Australia, Special Publication* **4**, 141–155.

Helby R, Morgan R & Partridge A D 1987. A palynological zonation of the Australian Mesozoic. *Memoir of the Association of Australasian Palaeontologists* **4**, 94 p.

Hill R S 1998. Fossil evidence for the onset of xeromorphy and scleromorphy in Australian Proteaceae. *Australian Systematic Botany* **11**, 391–400.

Hill R S & Merrifield H E 1993. An Early Tertiary macroflora from West Dale, southwestern Australia. *Alcheringa* **17**, 285–326.

Hill R S, Hill K E, Carpenter R J & Jordan G J 2019. New macrofossils of the Australian cycad *Bowenia* and their significance in reconstructing the past morphological range of the genus. *International Journal of Plant Sciences* **180**, 128–140.

Hocking R M & Preston W A 1998. Western Australia: Phanerozoic geology and mineral resources. *BMR Journal of Australian Geology and Geophysics* **17**, 245–260.

Hull P M & Darroch S A F 2013. Mass extinctions and the structure and function of ecosystems. *The Paleontological Society Papers* **19**, 115–156.

Itzstein-Davey F 2004. An early Holocene palaeoenvironmental record from Two Mile Lake, south-western Australia. *Australian Geographer* **35**, 317–332.

Jansonius J & McGregor D C 1996. *Palynology: principles and applications*. American Association of Stratigraphic Palynologists Foundation Contributions Series, Dallas, 1330 p.

Jones T P & Rowe N P, editors 1999 *Fossil Plants and Spores: Modern Techniques*. Geological Society, London, 396 p.

Kennaway G M, Eaton G L & Feist-Burkhardt S 2008. A detailed protocol for the preparation and orientation of single fossil dinoflagellate cysts for transmission electron microscopy. *Palynology* **32**, 1–15.

Kemp E M, Balme B E, Helby R J, Kyle R A, Playford G & Price P L 1977. Carboniferous and Permian palynostratigraphy in Australia and Antarctica: A review. *BMR Journal of Australian Geology and Geophysics* **2**, 177–208.

Kesseler R & Harley M M 2008. *Pollen, the hidden sexuality of flowers*. Papadakis Publisher, London, 264 p.

Korasidis V A, Wagstaff B E, Gallagher S J, Duddy I R, Tosolini A-M P, Cantrill D J & Norvick M S 2016. Early angiosperm diversification in the Albian of southeast Australia: implications for flowering plant radiation across eastern Gondwana. *Review of Palaeobotany and Palynology* **232**, 61–80.

Kustatscher E, Ash S R, Karasev E, Pott C, Vajda V, Yu J & McLoughlin S 2018. Flora of the Late Triassic. Pages 545–622 in Tanner L H editor *The Late Triassic World. Earth in a Time of Transition*. Topics in Geobiology **46**, Springer, Cham, Switzerland, DOI: 10.1007/978-3-319-68009-5_13

Lang W H & Cookson, I C 1935. On a flora, including vascular land plants, associated with *Monograptus*, in rocks of Silurian age, from Victoria, Australia. *Philosophical Transactions of the Royal Society of London* **224B**, 421–449.

Mack C L & Milne L A 2015. Eocene palynology of the Mulga Rocks deposits, southern Gunbarrel Basin, Western Australia. *Alcheringa* **39**, 444–458.

Mack C L & Milne L A 2016. New *Banksieaeidites* species and pollen morphology in *Banksia*. *Australian Systematic Botany* **29**, 303–323.

Macphail M K 1997. Late Neogene climates in Australia: fossil pollen- and spore-based estimates in retrospect and prospect. *Australian Journal of Botany* **45**, 425–464.

Macphail M K 1999. Palynostratigraphy of the Murray Basin, inland southeastern Australia. *Palynology* **23**, 197–240.

Martin A R H 1995. Palaeogene proteaceous pollen and phylogeny. *Alcheringa* **19**, 27–40.

Martin H A & McMinn A 1994. Late Cainozoic vegetation history of north-western Australia, from the palynology of a deep-sea core (ODP Site 765). *Australian Journal of Botany* **42**, 95–102.

Martin J R, Redfern J, Horstwood M S A, Mory A J & Williams B P J 2019. Detrital zircon age and provenance constraints on late Paleozoic ice-sheet growth and dynamics in Western and central Australia. *Australian Journal of Earth Sciences* **66**, 183–207.

McLoughlin S 1992a. Permian sphenophytes from the Collie and Perth basins, Western Australia. *Review of Palaeobotany and Palynology* **75**, 153–182.

McLoughlin S 1992b. Western Australia's Permian plants. *The Fossil Collector Bulletin* **38**, 25–31.

McLoughlin S 1993. Plant fossil distributions in some Australian Permian non-marine sediments. *Sedimentary Geology* **85**, 601–619.

McLoughlin S 1995. New records of *Bergiopteris* and glossopterid fructifications from the Permian of Western Australia and Queensland. *Alcheringa* **19**, 175–192.

McLoughlin, S. 1996. Early Cretaceous macrofloras of Western Australia. *Records of the Western Australian Museum* **18**, 19–65.

McLoughlin, S. 2001. The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. *Australian Journal of Botany* **49**, 271–300.

McLoughlin S & Guppy L 1993. Western Australia's Cretaceous floras. *The Fossil Collector Bulletin* **39**, 11–21.

McLoughlin S & Hill R S 1996. The succession of Western Australian Phanerozoic terrestrial floras. Pages 61–80 in Hopper S D, Chappill J A, Harvey M S & George AS, editors, *Gondwanan Heritage: Past, Present and Future of the Western Australian Biota*. Surrey Beatty & Sons, Chipping Norton, Australia.

McLoughlin S & McNamara K 2001. *Ancient floras of Western Australia*. Western Australian Museum, Perth, Western Australia, 42 p.

McLoughlin S & Pott C 2009. The Jurassic flora of Western Australia. *GFF* **131**, 113–136.

McLoughlin S, Haig D W, Backhouse J, Holmes M A, Ellis G, Long J A & McNamara K J 1995. Oldest Cretaceous sequence, Giralia Anticline, Carnarvon Basin, Western Australia: late Hauterivian–Barremian. *AGSO Journal of Australian Geology and Geophysics* **15**, 445–468.

McLoughlin S, Lindström S & Drinnan A N 1997. Gondwanan floristic and sedimentological trends during the Permian–Triassic transition: new evidence from the Amery Group, northern Prince Charles Mountains, East Antarctica. *Antarctic Science* **9**, 281–298.

McLoughlin S, Tosolini A-M, Nagalingum N & Drinnan A N 2002. The Early Cretaceous (Neocomian) flora and fauna of the lower Strzelecki Group, Gippsland Basin, Victoria, Australia. *Association of Australasian Palaeontologists Memoirs* **26**, 144 p.

McLoughlin S, Martin S K & Beattie R 2015. The record of Australian Jurassic plant-arthropod interactions. *Gondwana Research* **27**, 940–959.

Milne L A 1988. Palynology of a late Eocene lignitic sequence from the western margin of the Eucla Basin, Western Australia. *Association of Australasian Palaeontologists, Memoir* **5**, 285–310.

Milne L A 1994. Relationship between *Propylipollis annularis* (Tertiary dispersed pollen) and extant *Xylomelum* (Proteaceae). Pages 193–213 *in* Kurmann M H & Doyle J A, editors, *Ultrastructure of Fossil Spores and Pollen*. Royal Botanic Gardens, Kew.

Milne L A 1998a. Surface-embedding of fossil pollen for time- and cost-effective ultramicrotomy (TEM) and multiple microscopy of single grains. *American Association of Stratigraphic Palynologists Foundation, Contributions Series* **33**, 95–105.

Milne L A 1998b. Tertiary palynology: *Beaupreaidites* and new Conospermeae (Proteoideae) affiliates. *Australian Systematic Botany* **11**, 553–603.

Milne L A 2018. Mullaloo Aquifer Project Palynology Report May 2018 for CSIRO Perth (unpublished).

Milne L A & Martin A R H 1998. Conospermeae pollen morphology and its phylogenetic implications. *Australian Systematic Botany* **11**, 503–552.

Moore P D, Webb J A & Collinson M E 1991. *Pollen Analysis*: second edition. Blackwell, Oxford, 216 p.

Mory A J 2017. *A Paleozoic perspective of Western Australia*. Geological Survey of Western Australia, Perth, 58 p.

Newsome J C & Pickett E J 1993. Palynology and palaeoclimatic implications of two Holocene sequences from southwestern Australia, *Palaeogeography, Palaeoclimatology, Palaeoecology* **101**, 245–261.

Peyrot D, Barrón E, Comas-Rengifo M J, Thouand E & Tafforeau P 2007. A confocal laser scanning and conventional wide field light microscopy study of *Classopollis* from the Toarcian-Aalenian of the Fuentelsaz section (Spain). *Grana* **20**, 217–226.

Peyrot D, Barrón E, Polette F, Batten D J & Néraudeau D 2019. Early Cenomanian palynofloras and inferred resiniferous forests and vegetation types in Charentes (southwestern France). *Cretaceous Research* **94**, 168–189.

Peyrot D, Keep M, Scibiorski J, McCartain E, Baille P, Soares J, Haig D W & Mory A J 2019. The Foura Sandstone type section (*Samaropollenites speciosus* Zone, Carnian–early Norian; early Late Triassic), Timor-Leste: preliminary correlation between Timor and the Bonaparte Basin: Australian Exploration Geoscience Convention, 2–5 September 2019, Perth, extended abstract 291, 5 p.

Phipps D & Playford G 1984. Laboratory techniques for extraction of palynomorphs from sediments. *Papers of the Department of Geology, The University of Queensland* **11**, 1–23.

Playford G 1971. Lower Carboniferous spores from the Bonaparte Gulf Basin, Western Australia and Northern Territory. *Bureau of Mineral Resources, Geology and Geophysics, Bulletin* **115**, 105 p.

Playford G 1972. Trilete spores of *Umbonatisporites* in the Lower Carboniferous of northwestern Australia. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **141**, 301–315.

Playford G 1976. Plant microfossils from the Upper Devonian and Lower Carboniferous of the Canning Basin, Western Australia, *Palaeontographica Abteilung B* **158**, 71 p.

Playford G 1982. A latest Devonian palynoflora from the Buttons Beds, Bonaparte Gulf Basin, Western Australia. *BMR Journal of Australian Geology and Geophysics* **7**, 149–157.

Playford G 2015. Mississippian palynoflora from the northern Perth Basin, Western Australia: systematics and stratigraphical and palaeogeographical significance. *Journal of Systematic Palaeontology*, DOI: 10.1080/14772019.2015.1091792 (30 October 2015); printed subsequently (December 2016) **14**, 731–770.

Playford G & Mory A J 2017. Composition and occurrence of the *Grandispora maculosa* zonal assemblage (Mississippian) in the subsurface of the Carnarvon Basin and the Coolcalalaya Sub-basin of Western Australia, and its Gondwanan distribution. *Rivista Italiana di Paleontologia e Stratigrafia* **123**, 275–318.

Playford G & Satterthwait D F 1985. Lower Carboniferous (Viséan) spores of the Bonaparte Gulf Basin, northwestern Australia. Part one. *Palaeontographica, Abteilung B* **195**, 125–152.

Playford G & Satterthwait D F 1986. Lower Carboniferous (Viséan) spores of the Bonaparte Gulf Basin, northwestern Australia. Part two. *Palaeontographica, Abteilung B* **200**, 1–32.

Playford G & Satterthwait D F 1988. Lower Carboniferous (Viséan) spores of the Bonaparte Gulf Basin, northwestern Australia. Part three. *Palaeontographica, Abteilung B* **208**, 1–26.

Powis G D 1984. Palynostratigraphy of the Late Carboniferous sequence, Canning Basin, WA, Pages 429–438 *in* Purcell P G, editor, *The Canning Basin W A. Proceedings Geological Society of Australia/Petroleum Exploration Society of Australia Symposium, Perth.*

Price P L & Filatoff J 1990. Application of morphological lineages in Australian palynostratigraphy. *Review of Palaeobotany and Palynology* **65**, 195–207.

Quinney A, Mays C, Stilwell J D, Zelenitsky D K & Therrien F 2015. The range of bioinclusions and pseudoinclusions preserved in a New Turonian (~90 Ma) amber occurrence from southern Australia. *Plos One*, DOI: 10.1371/journal.pone.0121307

Retallack G J 1977. Reconstructing Triassic vegetation of eastern Australasia: a new approach for the biostratigraphy of Gondwanaland. *Alcheringa* **1**, 247–278.

Retallack G J 1980. Late Carboniferous to Middle Triassic megafossil floras from the Sydney Basin. Pages 384–430 *in* Herbert C & Helby R J, editors, *A Guide to the Sydney Basin. Geological Survey of New South Wales, Bulletin* **26**.

Retallack G J 1995a. An Early Triassic fossil flora from the Culvida Soak, Canning Basin, Western Australia. *Journal of the Royal Society of Western Australia* **78**, 57–66.

Retallack G J 1995b. Permian–Triassic life crisis on land. *Science* **267**, 77–80.

Retallack G J, Veevers J J & Morante R 1996. Global coal gap between Permian-Triassic extinction and Middle Triassic recovery of peat-forming plants. *Geological Society of America, Bulletin* **108**, 195–207.

Retallack G J, Sheldon N D, Carr P F, Fanning M, Thompson C A, Williams M L, Jones B G & Hutton A 2011. Multiple Early Triassic greenhouse crises impeded recovery from Late Permian mass extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology* **308**, 233–251.

Rigby J F 1966. The Lower Gondwana floras of the Perth and Collie Basins, Western Australia. *Palaeontographica* **118B**, 113–152.

Rigby J F 1993. Plants. Pages 77–83 *in* Skwarko S K, editor, *Palaeontology of the Permian of Western Australia. Geological Survey of Western Australia, Bulletin* **136**.

Rubinstein C V & Vajda V 2019. Baltica cradle of early land plants? Oldest record of trilete spores and diverse cryptospore assemblages; evidence from Ordovician successions of Sweden. *GFF*, DOI: 10.1080/11035897.2019.1636860

Rubinstein C V, Gerrienne P, de la Puente G S, Astini R A & Steemans P 2010. Early Middle Ordovician evidence for land plants in Argentina (eastern Gondwana). *New Phytologist* **188**, 365–369.

Satterthwait D F & Playford G 1986. Spore tetrad structures of possible hepatic affinity from the Australian Lower Carboniferous. *American Journal of Botany* **73**, 1319–1331.

Sauquet H, Weston P H, Barker N P, Anderson C L, Cantrill D J & Savolainen V 2009. Using fossils and molecular data to reveal the origins of the Cape proteas (subfamily Proteoideae). *Molecular Phylogenetics and Evolution* **51**, 31–43.

Schopf J M 1975. Modes of fossil preservation. *Review of Palaeobotany and Palynology* **20**, 27–53.

Scibiorski J P, Peyrot D, Bourget J, Payenberg T & Charles A 2018. Palynology and palynofacies associations of Late Triassic assemblages from the Mungaroo Formation, Greater Gorgon Area, Western Australia. Royal Society of Western Australia Symposium: Landscapes, Seascapes & Biota: Unique WA — Past, Present & Future, 27–28 July 2018, Perth, Australia (poster presentation).

Scriven L J, McLoughlin S & Hill R S 1995. *Nothofagus plicata* (Nothofagaceae), a new deciduous Eocene macrofossil species, from southern continental Australia. *Review of Palaeobotany and Palynology* **86**, 199–209.

Sniderman J M K, Woodhead J D, Hellstrom J, Jordan G J, Drysdale R N, Tyler J J & Porch N 2016. Pliocene reversal of late Neogene aridification. *Proceedings of the National Academy of Sciences, U.S.A.* **113**, 1999–2004.

Sniderman J M K, Hellstrom J, Woodhead J D, Drysdale R N, Bajol P, Archer M & Hatcher L 2019. Vegetation and climate change in southwestern Australia during the Last Glacial Maximum. *Geophysical Research Letters* **46**, 1–12.

Spaak G, Edwards D S, Foster C B, Pagès A, Summons R E, Sherwood N & Grice K, 2017. Environmental conditions and microbial community structure during the Great Ordovician Biodiversification Event; a multi-disciplinary study from the Canning Basin, Western Australia. *Global and Planetary Change* **159**, 93–112.

Steemans P & Wellman C H 2004. Miospores and the emergence of land plants. Pages 361–366 *in* Webby B, Paris F, Droser M L & Percival I G editors *The Great Ordovician Biodiversification Event*. Columbia University Press, New York.

Stewart W N & Rothwell G W 1993. *Paleobotany and the Evolution of Plants*: second edition. Cambridge University Press, Cambridge.

Stover LE & Partridge AD 1982. Eocene spore-pollen from the Werillup Formation, Western Australia. *Palynology* **6**, 69–96.

Sun Y, Joachimski M M, Wignall P B, Yan C, Chen Y, Jiang H, Wang L & Lai X 2012. Lethally hot temperatures during the Early Triassic greenhouse. *Science* **338**, 366–370.

Taylor T N, Taylor E L & Krings M 2009. *Paleobotany. The Biology and Evolution of Fossil Plants*. Elsevier, Amsterdam, 1230 p.

Tosolini A-M P, McLoughlin S, Wagstaff B E, Cantrill D J & Gallagher S J 2015. Cheirolepidiacean foliage and pollen from Cretaceous high-latitudes of southeastern Australia. *Gondwana Research* **27**, 960–977.

Traverse A 2007. *Paleopalynology*: second edition. Springer, Dordrecht, 772 p.

Tyler M J & Prideaux G J 2016. Early to middle Pleistocene occurrences of *Litoria*, *Neobatrachus* and *Pseudophryne* (Anura) from the Nullarbor Plain, Australia: first frogs from the "frog-free zone". *Memoirs of Museum Victoria* **74**, 403–408.

van der Kaars S, Wang X, Kershaw P, Guichard F & Duddy A S 2000. A Late Quaternary palaeoecological record from the Banda Sea, Indonesia: patterns of vegetation, climate and biomass burning in Indonesia and northern Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **155**, 135–153.

Vajda V & McLoughlin S 2007. Extinction and recovery patterns of the vegetation across the Cretaceous–Palaeogene boundary—a tool for unravelling the causes of the end-Permian mass-extinction. *Review of Palaeobotany and Palynology*, **144**, 99–112.

Villanueva-Amadoz U, Benedetti A, Mendez J & Diez J B 2012. Focused ion beam nano-sectioning and imaging: A new method in characterisation of palaeopalynological remains. *Grana* **51**, 1–9.

Willis K J & McElwain J C 2002. *The Evolution of Plants*. Oxford University Press, Oxford.

White M E & Yeates A N 1976. Plant fossils from the northeastern part of the Canning Basin, Western Australia. *Bureau of Mineral Resources, Geology and Geophysics, Record* **1976/018**, 32 p.

Wood G D, Gabriel A M & Lawson J C 1996. Palynological techniques, processing and microscopy. Pages 29–50 *in* Jansonius J & McGregor D C, editors, *Palynology: Principles and Applications*. American Association of Stratigraphic Palynologists Foundation, Dallas.

Yasin A R & Mory A J (compilers) 1999. Coburn 1 well completion report, Gascoyne Platform, Southern Carnarvon Basin, Western Australia: *Geological Survey of Western Australia Record*, 99 p.

Appendix 1.

Information (age, stratigraphy, location and source) relative to the localities and petroleum wells mentioned in the text.

Table 1

Localities, stratigraphic units and ages for the figured specimens.

Taxa	Figure	Locality	Depth (m)	Unit	Age	Reference (or location of specimen)
Velatitetras laevigata	2A	Theia 1	1217.67–17.7	Goldwyer Fm	Early–Middle Ordovician	Spaak *et al.* (2017)
indeterminate cryptospore	2B	Theia 1	1217.67–17.7	Goldwyer Fm	Early–Middle Ordovician	Spaak *et al.* (2017)
Geminospora lemurata	2C,D			Gneudna Fm	Frasnian (Late Devonian)	uncatalogued, at UWA
Rhabdosporites langii	2E	BMR 2 Laurel Downs	517.2–20.3	Fairfield Group	late Famennian (Late Devonian)	Balme & Hassell (1962)
Verrucosisporites scurrus	2F			Gneudna Fm	Frasnian (Late Devonian)	uncatalogued, Balme (1988)
Emphanisporites annulatus	2G			Gneudna Fm	Frasnian (Late Devonian)	uncatalogued, at UWA
Emphanisporites rotatus	2H	Uranerz CDH8		Gneudna Fm	Frasnian (Late Devonian)	Balme (1988)
Gneudnaspora divellomedia	2I	Aquitaine DDH4		Gneudna Fm	Frasnian (Late Devonian)	Balme (1988)
Ancyrospora langii	2J			Gneudna Fm	Frasnian (Late Devonian)	uncatalogued, at UWA
Retispora lepidophyta	2K	Stumpy Soak 2	25.6	Fairfield Group	late Famennian (Late Devonian)	Balme & Hassell (1962)
Convolutispora fromensis, holotype	2L	Frome Rocks 2	1310.6–12.1	Luluigui Fm	late Famennian (Late Devonian)	Balme & Hassell (1962)
Granulatisporites frustulentus, holotype	2M	BMR 2 Laurel Downs	514.4–17.2	Fairfield Group	late Famennian (Late Devonian)	Balme & Hassell (1962)
Claytonispora distincta	2N	Meda 1	1541–43	Laurel Fm	Early Carboniferous (~Tournaisian)	Playford (1972)
Diatomozonotriletes birkheadensis	2O	YCH 2	170.1	?Nangetty Fm	mid-Carboniferous	Playford (2015), Playford & Mory (2017)
Anapiculatisporites amplus	2P	YCH 2	118.8	?Nangetty Fm	mid-Carboniferous	Playford (2015), Playford & Mory (2017)
Raistrickia accincta	2Q	YCH 2	170.1	?Nangetty Fm	mid-Carboniferous	Playford (2015), Playford & Mory (2017)
Raistrickia corymbiata, holotype	2R	YCH 2	170.1	?Nangetty Fm	mid-Carboniferous	Playford (2015), Playford & Mory (2017)
Reticulatisporites magnidictyus	2S	Minderoo 1	607.2	?Quail Fm	mid-Carboniferous	Playford (2015), Playford & Mory (2017)
Auroraspora solisorta	2T	Gnarloo 1	476.4	?Quail Fm	mid-Carboniferous	Playford & Mory (2017)
Grandispora maculosa	3A	DDH CL5	179.8	?Nangetty Fm	mid-Carboniferous	Playford (2015)
Psomospora detecta	3B	YCH 2	118.8	?Nangetty Fm	mid-Carboniferous	Playford (2015), Playford & Mory (2017)
Indotriradites daemonii	3C	DDH CL5	179.8	?Nangetty Fm	mid-Carboniferous	Playford (2015)
Indotriradites kuttungensis	3D	YCH 2	231.5	?Nangetty Fm	mid-Carboniferous	Playford (2015), Playford & Mory (2017)
Velamisporites cortaderensis	3E	DDH CL5	179.8	?Nangetty Fm	mid-Carboniferous	Playford (2015)
Verrucosisporites quasigobbettii	3F	DDH CL5	179.8	?Nangetty Fm	mid-Carboniferous	Playford (2015)
Spelaeotriletes ybertii	3G	Blackstone 1	1448.8–62.1	Reeves Fm	mid-Carboniferous	slide held by GSWA (WAPIMS)
Plicatipollenites sp.	3H	Scarpia 1	1459	Anderson Fm	Early Carboniferous (~Visean)	slide held by GSWA (WAPIMS)
Potonieisporites sp.	3I	Scarpia 1	1459	Anderson Fm	Early Carboniferous (~Visean)	slide held by GSWA (WAPIMS)
Calamospora sp.	3J	Scarpia 1	1459	Anderson Fm	Early Carboniferous (~Visean)	slide held by GSWA (WAPIMS)
Punctatisporites gretensis	3K	Hebburn No. 2 Colliery, NSW.		Main Greta Seam	late Early Permian	rephotographed holotype (slide held by UWA)
Secarisporites sp.	3L	Blackstone 1	1448.8–62.1	Reeves Fm	mid-Carboniferous	slide held by GSWA (WAPIMS)
Protohaploxypinus samoilovichii	3M	outcrop		Kockatea Shale	Early Triassic	Haig *et al.* (2015)
Dulhuntyispora parvithola	3N	Pyramid Bore	undiff. cuttings	Hardman Fm	Middle–Late Permian	GSWA sample 185801
Horriditriletes tereteangulatus	3O	Fraser River 1	574.5	Grant Group	Early Permian	slide held by GSWA (WAPIMS)
Microbaculispora tentula	3P	Point Moody 1	838.2–51.2	Grant Group	~Early Permian	slide held by GSWA (WAPIMS)
Lundbladispora willmotii	3Q	Lynher 1	2682–697.5	Nome Fm	Late Triassic	slide held by GSWA (WAPIMS)

Table 1. (cont.)

Taxa	Figure	Locality	Depth (m)	Unit	Age	Reference (or location of specimen)
Kraeuselisporites cuspidus	3R	Batavia 1	2565 m	Kockatea Shale	Early Triassic	Geoscience Australia, slide 1977430
Aratrisporites banksii	3S	ODP-760A	380.6	Mungaroo Fm	Late Triassic	slide held by Chevron Australia
Falcisporites australis	3T	Roc 1	3360–70 m	Keraudren Fm	Early Triassic	slide held by GSWA (WAPIMS)
Lepidodendroid lycopsid trunk	4A	outcrop	–	Kellys Knob Ss	Frasnian (Late Devonian)	Mory & Beere (1988)
Ottokaria bullata	4B	Irwin River (N Branch)	–	Irwin River CM	Early Permian	McLoughlin (1995)
Raniganjia minima	4C	Muja pit, Collie	–	Muja CM	Middle Permian	McLoughlin (1992)
Paracalamites australis	4D	Stockton pit, Collie	–	Ewington CM	Early Permian	specimen held by NRM
Glossopteris sp.	4E	Stockton pit, Collie	–	Ewington CM	Early Permian	specimen held by NRM
Sphenophyllum morganae	4F	Irwin River (N Branch)	–	Irwin River CM	Early Permian	McLoughlin (1992)
Liknopetalon sp.	4G	Irwin River (N Branch)	–	Irwin River CM	Early Permian	Adendorff *et al.* (2003)
Gondwanophyton daymondii	4H	Irwin River (N Branch)	–	Irwin River CM	Early Permian	McLoughlin (1992)
Noeggerathiopsis sp.	4I	Muja pit, Collie	–	Muja CM	Middle Permian	McLoughlin & McNamara (2001)
Vertebraria australis	4J	Mount Talbot	–	Condren Ss	Middle Permian	specimen held by NRM
Bergiopteris sp. cf. *B. archangelskyi*	4K	Irwin River (S Branch)	–	Wagina Ss	Late Permian	McLoughlin (1995)
Sphenophyllum rhodesii	4L	Irwin River (N Branch)	–	Irwin River CM	Early Permian	McLoughlin (1992)
Ephedripites macistriatus	5A	ODP-760A	241	Mungaroo Fm	Late Triassic	slide held by Chevron Australia
Minutosaccus crenulatus	5B	ODP-760A	241	Mungaroo Fm	Late Triassic	slide held by Chevron Australia
Samaropollenites speciosus	5C	ODP-760A	94.13	Mungaroo Fm	Late Triassic	slide held by Chevron Australia
Aulisporites astigmosus	5D	ODP-760B	380.6	Mungaroo Fm	Late Triassic	slide held by Chevron Australia
Classopollis sp	5E, F	Badaminna 1	1543.8	Cattamarra CM	Early Jurassic	slide held by UWA
Callialasporites turbatus	5G	Badaminna 1	1148.3	Cadda Fm	Middle Jurassic	slide held by UWA
Callialasporites dampieri	5H	Badaminna 1	1413.9	Cattamarra CM	Early–Middle Jurassic	slide held by UWA
Araucariacites australis	5I	Gingin 1	1412	Yarragadee Fm	Late Jurassic	slide held by UWA
Ischyosporites marburgensis	5J, K	Badaminna 1	1303.6	Cattamarra CM	Early–Middle Jurassic	slide held by UWA
Matonisporites crassiangulatus	5L	Hill River 2A	80.9	Cattamarra CM	Early–Middle Jurassic	slide held by UWA
Cyathidites minor	5M	Badaminna 1	694.9	Yarragadee Fm	Late Jurassic	slide held by UWA
Osmundacidites welmanii	5N	Badaminna 1	1543.8	Cattamarra CM	Early Jurassic	slide held by UWA
Microcachryidites antarcticus	5O	BH16	27.07	Warnbro Group	Early Cretaceous	slide to be submitted to GSWA
Staplinisporites caminus	5P	Investigator 1	1635	Barrow Group	Early Cretaceous	slide held by GSWA (WAPIMS)
Foveosporites subtriangularis	5Q	Harvey 1	165–180	Leederville Fm	Early Cretaceous	slide held by GSWA (WAPIMS)
Retitriletes circolumenus	5R, S	Investigator 1	1513	Barrow Group	Early Cretaceous	slide held by GSWA (WAPIMS)
Retitriletes clavatoides	5T	Investigator 1	1513	Barrow Group	Early Cretaceous	slide held by GSWA (WAPIMS)
cf. *Nymboidiantum multilobatum*	6A	Glengarry near Geraldton		Kockatea Shale	Early Triassic	Haig *et al.* (2015)
Sphenopteris sp.	6B	5 km N of Mingenew	–	Yarragadee Fm	Late Jurassic	McLoughlin & Pott (2009)
Pagiophyllum amanguanus	6C	6 km N of Mingenew	–	Yarragadee Fm	Late Jurassic	McLoughlin & Pott (2009)
Otozamites linearis	6D	7 km N of Mingenew	–	Yarragadee Fm	Late Jurassic	McLoughlin & Pott (2009)
Elatocladus confertus	6E	8 km N of Mingenew	–	Yarragadee Fm	Late Jurassic	McLoughlin & Pott (2009)
Ptilophyllum cutchense	6F	9 km N of Mingenew	–	Yarragadee Fm	Late Jurassic	McLoughlin & Pott (2009)
Isoetites elegans	6G	near Gingin	–	Leederville Fm	Early Cretaceous	Walkom (1944)
Hausmannia sp.	6H	near Gingin	–	Leederville Fm	Early Cretaceous	Walkom (1944)
megaspores associated with *Isoetites elegans*	6I	Gantheaume Point	–	Broome Ss	Early Cretaceous	McLoughlin (1996)
Ptilophyllum cutchense	6J	near Gingin	–	Leederville Fm	Early Cretaceous	McLoughlin (1996)
Taeniopteris daintreei	6K	WAPET outcrop NH3	–	Nanutarra Fm	Early Cretaceous	not previously illustrated

Table 1. (cont.)

Taxa	Figure	Locality	Depth (m)	Unit	Age	Reference (or location of specimen)
Cladophlebis sp. cf. *C. oblonga*	6L	Gantheaume Point	–	Broome Ss	Early Cretaceous	McLoughlin (1996)
Ptilophyllum acutifolium	6M	Jubrico Creek		Nanutarra Fm	Early Cretaceous	McLoughlin (1996)
Nathorstianella babbagensis	6N	Gantheaume Point	–	Broome Ss	Early Cretaceous	McLoughlin (1996)
Komlopteris sp. cf. *K. indica*	6O	near Gingin	–	Leederville Fm	Early Cretaceous	McLoughlin (1996)
Proteacidites carobelindiae	7A–C	Balladonia 15	63	?Pallinup Fm	late Eocene	Milne (1998)
Proteacidittes carobelindiae	7D	Zanthus 11	39	?Pallinup Fm	late Eocene	sample held by Curtin
Proteacidites palisadus	7E, F	Mullalo Production Bore 02/13	33–36	Kings Park Fm	late Paleocene	Milne (2018)
Proteacidites annularis	7G	Zanthus 11	37	?Pallinup Fm	late Eocene	sample held by Curtin
Proteacidites adenanthoides	7H	Mullalo Production Bore 02/13	156–159	?Poison Hill Gs	Late Cretaceous	Milne (2018)
Clavifera triplex	7I	Mullalo Production Bore 02/13	156–160	?Poison Hill Gs	Late Cretaceous	Milne (2018)
Phyllocladidites mawsonii	7J	Zanthus 11	41	?Pallinup Fm	late Eocene	Carpenter & Milne (in press)
Lygistepollenites florinii	7K	Mulga Rock	53.9	unamed	late Eocene	Mack (2016)
Nothofagidites cf. *emarcidus*	7L	Lake Wells	123.8–124	unamed	Miocene – lower Pliocene	sample held by Curtin
Haloragacidites harrisii	7M	Lake Wells	119.9–112	unamed	Miocene – lower Pliocene	sample held by Curtin
Anacolosidites acutullus	7N	Zanthus 11	39	?Pallinup Fm	late Eocene	sample held by Curtin
Proteacidites punctiporus	7O	Zanthus 11	37	?Pallinup Fm	late Eocene	sample held by Curtin
Proteacidites cumulus	7P	Zanthus 11	41	?Pallinup Fm	late Eocene	sample held by Curtin
Proteacidites reticulatus	7Q	Zanthus 11	38	?Pallinup Fm	late Eocene	sample held by Curtin
Milfordia homeopunctata	7R	Zanthus 11	41	?Pallinup Fm	late Eocene	sample held by Curtin
Myrtaceidites eucalyptoides	7S	Lake Wells	119.9–112	unamed	Miocene – lower Pliocene	sample held by Curtin
Eucalyptus marginata	7T	South West		unamed	Holocene	sample held by Curtin
probably *Agathis*	8A	Muir-Unicup core MU11	22.19–22.23	unnamed	Cenozoic (late Eocene)	Al-Shawareb (2009)
Dacrycarpus vieillardii	8B	New Caledonia			modern	NA
Dacrycarpus sp.	8C	Muir-Unicup core MU11	72.8–72.9	Werillup Fm	Cenozoic (late Eocene)	Al-Shawareb (2009)
Dacrydium sp.	8D	Muir-Unicup core MU11	22.6–22.63	Werillup Fm	Cenozoic (late Eocene)	Al-Shawareb (2009)
Nothofagus plicata	8E	Walebing		Kojonup Ss	Cenozoic (late Eocene)	uncatalogued
Nothofagus alpina	8F	southern South America			modern	NA
Bowenia spectabilis	8G	Daintree rainforest, Queensland			modern	NA
Bowenia sp.	8H	Muir-Unicup core MU11	22.19–22.23	Werillup Fm	Cenozoic (late Eocene)	Al-Shawareb (2009)
Persoonieae	8I	Muir-Unicup core MU11	22.88–22.97	Werillup Fm	Cenozoic (late Eocene)	Al-Shawareb (2009)
Banksia-like foliage	8J	Muradup		Kojonup Ss	Cenozoic (late Eocene)	specimen held by UWA
B. candolleana	8K	Southwestern Australia			modern	NA
B. paleocrypta	8L	Walebing		Kojonup Ss	Cenozoic (late Eocene)	unregistered, Carpenter *et al.* (2014)
B. menziesii	8M	Southwestern Australia			modern	NA

CM - coal measures   Curtin - Curtin University
Fm - Formation   GSWA - Geological Survey of Western Australia http://dmp.wa.gov.au/Petroleum-and-Geothermal-1497.aspx
Gs - Greensand   NRM - Swedish Museum of Natural History
Ss - Sandstone   UWA - E. de C.C. Earth Science Museum, The University of Western Australia

REFERENCES

ADENDORFF R, BAMFORD M K & McLOUGHLIN S 2003. *Liknopetalon*: a review of a rare Gondwanan, Permian pteridophyte. *Review of Palaeobotany and Palynology* **126**, 83–101.

AL-SHAWAREB A 2009. Eocene palynology of a lignite section in the Muir-Unicup Catchment, Werillup Formation, south Western Australia. *BSc Honours Thesis, University of Western Australia*, 1–98 (unpublished).

BALME B E 1988. Miospores from Late Devonian (early Frasnian) strata, Carnarvon Basin, Western Australia. *Palaeontographica Abteilung B* **209**, 109–166.

BALME B E & HASSELL C W 1962. Upper Devonian spores from the Canning Basin, Western Australia. *Micropaleontology* **8**, 1–28.

CARPENTER R J, McLOUGHLIN S, HILL R S, McNAMARA K J & JORDAN G J 2014. Early evidence of xeromorphy in angiosperms: stomatal encryption in a new Eocene species of *Banksia* (Proteaceae) from Western Australia. *American Journal of Botany* **101**, 1486–1497.

CARPENTER R J & MILNE L A in press. New species of xeromorphic *Banksia* (Proteaceae) foliage and *Banksia*-like pollen from the late Eocene of Western Australia. *Australian Journal of Botany*.

HAIG D W, MARTIN S K, MORY A, McLOUGHLIN S, BACKHOUSE J, BERRELL R, KEAR B P, HALL R, FOSTER C B, CHI G R & BEVAN J 2015. Early Triassic (early Olenekian) life in the interior of East Gondwana: mixed marine–terrestrial biota from the Kockatea Shale, Western Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **417**, 511–533.

MACK M L 2016. Palynology of the Narnoo palaeovalley, Western Australia, and its implications for the biostratigraphy and palaeovegetation of southern Australia. *PhD Thesis, Curtin University*, 226p. (unpublished).

McLOUGHLIN S 1992. Permian sphenophytes from the Collie and Perth basins, Western Australia. *Review of Palaeobotany and Palynology* **75**, 153–182.

McLOUGHLIN S 1995. New records of *Bergiopteris* and glossopterid fructifications from the Permian of Western Australia and Queensland. *Alcheringa* **19**, 175–192.

McLOUGHLIN S & McNAMARA K 2001. *Ancient floras of Western Australia*. Western Australian Museum, Perth, Western Australia.

McLOUGHLIN S & POTT C 2009. The Jurassic flora of Western Australia. *GFF* **131**, 113–136.

MILNE L A 1998. Surface-embedding of fossil pollen for time- and cost-effective ultramicrotomy (TEM) and multiple microscopy of single grains. *American Association of Stratigraphic Palynologists Foundation, Contributions Series* **33**, 95–105.

MILNE L A 2018. Mullaloo Aquifer Project Palynology Report May 2018 for CSIRO Perth (unpublished).

MORY A J & BEERE G M 1988. Geology of the onshore Bonaparte and Ord Basins in Western Australia. Geological Survey of Western Australia, Bulletin 134.

PLAYFORD G 2015. Mississippian palynoflora from the northern Perth Basin, Western Australia: systematics and stratigraphical and palaeogeographical significance. *Journal of Systematic Palaeontology*, doi: 10.1080/14772019.2015.1091792 (30 October 2015); printed subsequently (December 2016) **14**, 731–770.

PLAYFORD G & MORY, A J 2017. Composition and occurrence of the *Grandispora maculosa* zonal assemblage (Mississippian) in the subsurface of the Carnarvon Basin and the Coolcalalaya Sub-basin of Western Australia, and its Gondwanan distribution. *Rivista Italiana di Paleontologia e Stratigrafia* **123**, 275–318.

SPAAK G, EDWARDS D S, FOSTER C B, PAGÈS A, SUMMONS R E, SHERWOOD N & GRICE K, 2017. Environmental conditions and microbial community structure during the Great Ordovician Biodiversification Event; a multi-disciplinary study from the Canning Basin, Western Australia. *Global and Planetary Change* **159**, 93–112.

WALKOM A B 1944. Fossil plants from Gingin, W.A. *Journal of the Royal Society of Western Australia* **28**, 201–207.

Table 2.

Locations mentioned in text and Table 1 arranged by basin.

Basin	Petroleum well, mineral drillhole or locality	Sub-basin	Latitude (°S)	Longitude (°E)
Bonaparte	outcrop near Cockatoo Fault	Burt Range Sub-basin	15.916556	129.087528
Browse	Lynher 1	Barcoo Sub-basin	15.938714	121.084352
Canning	Blackstone 1	Lennard Shelf	17.585533	124.353049
Canning	BMR 2 Laurel Downs	Lennard Shelf	18.1183	125.3347
Canning	Culvida Soak	Gregory Sub-basin	~20.227	~126.929
Canning	Fraser River 1	Fitzroy Trough	17.416157	123.163617
Canning	Frome Rocks 2	Jurgurra Terrace	18.253879	123.661253
Canning	Gantheaume Point	Jurgurra Terrace	17.974300	122.177098
Canning	Meda 1	Lennard Shelf	17.397533	124.193587
Canning	Mount Talbot	Fitzroy Trough	18.85548	126.09332
Canning	Point Moody 1	Gregory Sub-basin	21.259444	127.806111
Canning	Pyramid Bore	Fitzroy Trough	18.359333	124.659333
Canning	Scarpia 1	Fitzroy Trough	18.052141	124.844624
Canning	Stumpy Soak 2 (water bore)	Lennard Shelf	~17.8	~125.1
Canning	Theia 1	Broome Platform	18.901072	123.293867
?Eucla	Mulga Rock	NA	~29.985	~123.81
Eucla	Zanthus 11	Balladonia Shelf	31.9371	123.4942
Northern Carnarvon	Investigator 1	Exmouth Plateau	20.350531	112.96841
Northern Carnarvon	Jubrico Creek	Peedamullah Shelf	22.5256	115.3202
Northern Carnarvon	Long Island 1	Barrow Sub-basin	21.619527	114.68939
Northern Carnarvon	Minderoo 1	Peedamullah Shelf	21.845944	115.079793
Northern Carnarvon	ODP 122-760A	Wombat Plateau	16.9220	115.5413
Northern Carnarvon	ODP 122-760B	Wombat Plateau	19.9207	112.2540
Northern Carnarvon	Onslow 1	Barrow Sub-basin	21.765225	114.875997
Northern Carnarvon	WAPET NH3	Peedamullah Shelf	22.14861	115.45694
overlies Yilgarn Craton	Lake Wells	NA	27.2339	122.9922
overlies Yilgarn Craton	Muir-Unicup core MU11	NA	34.339013	116.824689
overlies Yilgarn Craton	Muradup	NA	33.91	116.91
overlies Yilgarn Craton	Walebing	NA	30.69	116.225
overlies Yilgarn Craton	West Dale	NA	32.227	116.603
Perth	Badaminna 1	Dandaragan Trough	31.340721	115.668695
Perth	Batavia 1	Abrolhos Sub-basin	28.898403	114.261554
Perth	CRA Coolcalalaya YCH2	Coolcalalaya Sub-basin	27.731861	115.109067
Perth	DDH CL5	Irwin Terrace	28.369	115.411
Perth	Ewington open cut mine	Collie Sub-basin	33.21731	116.15039
Perth	Gingin 1	Beermullah Trough	31.143056	115.827222
Perth	Gingin, 3 km NNE of town	Beermullah Trough	31.324	115.9217
Perth	Glengarry, near Geraldton	Greenough Shelf	28.83	114.79
Perth	Harvey 1	Mandurah Terrace	32.991886	115.774489
Perth	Hill River 2A	Dandaragan Trough	30.182535	115.247214
Perth	Irwin R (N Branch)	Irwin Terrace	28.9386	115.5484
Perth	Irwin R (S Branch)	Irwin Terrace	28.9587	115.5545
Perth	Lanco Bunbury Port Engineering BH16	Bunbury Trough	33.4451389	115.685167
Perth	Mingenew, road cutting 5 km N of town	Wicherina Terrace	29.1454	115.4414
Perth	Muja Pit, Collie	Collie Sub-basin	33.25564	116.18788
Perth	Mullaloo Production Bore 02/13	Mandurah Terrace	31.99366	115.88298
Perth	Stockdale Pit, Collie	Collie Sub-basin	33.21731	116.15039
Perth	YCH 2	Coolcalalaya Sub-basin	27.718194	114.995917
Roebuck	Roc 1	Bedout Sub-basin	18.8807	118.8225
Southern Carnarvon	Aquitaine & Uranerz boreholes	Merlinleigh Sub-basin	23.6 – 24.1	115.1 – 115.2
Southern Carnarvon	Coburn 1	Gascoyne Platform	26.4203	114.1331
Southern Carnarvon	Gnaraloo 1	Gascoyne Platform	23.675645	113.786241
Southern Carnarvon	Yaringa 1	Gascoyne Platform	26.064852	114.36111

Appendix 2. Taxa cited in the main text and in explanations of figures 2–8. Megascopic remains are preceded by #, extant species or genera by ♦, and marine cysts by ◊.

♦ *Adenanthos* Labillardière, 1805

Anacolosidites acutullus Cookson & Pike, 1954

Agathis Salisbury, 1807

♦ *Anacolosa* (Blume, 1826) Blume, 1850

Anapiculatisporites amplus Playford & Powis, 1979

Anapiculatisporites concinnus Playford, 1962

Ancyrospora langii (Taugourdeau-Lantz, 1960) Allen, 1965

Aratrisporites banksii Playford, 1965

Araucaria Jussieu, 1789

Araucariacites australis Cookson, 1947 ex Couper, 1953

Araucarioxylon Kraus, 1870

Arberia White, 1908

Aulisporites astigmosus (Leschik, 1956) Klaus, 1960

Auroraspora solisorta Hoffmeister, Staplin & Malloy, 1955

Baculatisporites Pflug & Thomson, 1953

♦ *Banksia candolleana* Meissner, 1855

♦ *Banksia menziesii* R. Brown, 1830

♦ *Banksia nutans* R. Brown, 1810

Banksia paleocrypta Carpenter, McLoughlin, Hill, McNamara & Jordan, 2014

♦ *Banksia tricuspis* Meissner, 1855

Banksieaeidites Cookson, 1950

Baragwanathia longifolia Lang & Cookson, 1935

♦ *Beauprea spathulaefolia* Virot, 1968.

Beaupreaidites diversiformis Milne, 1998

Beaupreaidites elegansiformis Cookson, 1950 emend. Milne, 1998.

Bergiopteris sp. cf. *B. archangelskyi* Rigby, 1991

♦ *Bowenia spectabilis* W. Hooker ex J. Hooker, 1863

Calamospora Schopf, Wilson & Bentall, 1944

Callialasporites dampieri (Balme, 1957) Sukh Dev, 1961

Callialasporites turbatus (Balme, 1957) Schultz, 1967

♦ *Callitris preissii* Miquel, 1845

Calyptosporites proximocavatus Balme, 1988

Camerosporites Leschik, 1956

Classopollis Pflug, 1953

Cladophlebis sp. cf. *C. oblonga* Halle, 1913

Clavifera triplex (Bolkhovitina, 1953) Bolkhovitina, 1966

Claytonispora distincta (Clayton, 1971) Playford & Melo, 2012

Convolutispora fromensis Balme & Hassell, 1962

♦ *Corymbia calophylla* (Lindley, 1841) K.D.Hill & L.A.S. Johnson, 1995

Cristatisporites triangulatus (Allen, 1965) McGregor & Camfield, 1982

Cyathidites minor Couper, 1953

Cyclogranisporites R. Potonié & Kremp, 1954

Cymbosporites hormiscoides Balme, 1988

Dacrydium Solander, 1786 ex Lambert, 1807

Dacrycarpus vieillardii (Parlatore, 1868) de Laubenfels, 1969

Densoisporites Weyland & Krieger, 1953

Diatomozonotriletes birkheadensis Powis, 1984

Dicroidium Gothan, 1912

♦ *Doryanthes* Corrêa, 1802

Dulhuntyispora parvithola (Balme & Hennelly, 1956) Potonié, 1960

Elatocladus confertus (Oldham & Morris, 1863) Halle, 1913

♦ *Eucalyptus gomphocephala* de Candolle, 1828

♦ *Eucalyptus marginata* Smith, 1802

Glossopteris Brongniart, 1828 ex Brongniart, 1831

Gondwanophyton daymondii Rigby, 1993

Grandispora maculosa Playford & Helby, 1968

Granulatisporites frustulentus Balme & Hassell, 1962

♦ *Grevillea* R. Brown ex Knight, 1810

Haloragacidites harrisii (Couper, 1953) Harris, 1971

Hausmannia Dunker, 1846

♦ *Helicia* Loureiro, 1790

Horriditriletes tereteangulatus (Balme & Hennelly, 1956) Backhouse, 1991

Indotriradites daemonii Loboziak, Melo, Playford & Streel, 1999

Indotriradites kuttungensis (Playford & Helby, 1968) Playford, 1991

Infernopollenites Scheuring, 1970

Ischyosporites marburgensis de Jersey, 1963

Isoetites elegans Walkom, 1944

Kraeuselisporites cuspidus Balme, 1963

Komlopteris sp. cf. *K. indica* (Feistmantel, 1877) Barbacka, 1994

Lepidodendron Sternberg, 1820

Libocedrus Endlicher, 1847

Liknopetalon Smithies, 1985 emend. Adendorff, Bamford & McLoughlin, 2003

Lundbladispora willmotti Balme, 1963

Lygistepollenites florinii (Cookson & Pike, 1954) Stover & Evans, 1973

Matonisporites crassiangulatus (Balme, 1957) Dettmann, 1963

♦ *Macadamia* F. Mueller, 1857

♦ *Melaleuca* Linnaeus, 1767

Microbaculispora tentula Tiwari, 1965

Microcachryidites antarcticus Cookson, 1947

Minutosaccus crenulatus Dolby & Balme, 1976

◊ *Micrhystridium* Deflandre, 1937

Milfordia homeopunctata (McIntyre, 1965) Partridge, 1973

Myrtaceidites eucalyptoides Cookson & Pike, 1954

Nathorstianella babbagensis (Woodward, 1895) Glaessner & Rao, 1955

cf. *Nymboidiantum multilobatum* Holmes, 2003

Noeggerathiopsis Feistmantel, 1879

Nothofagidites sp. cf. *N. emarcidus* (Cookson, 1958) Harris, 1964

Nothofagus plicata Scriven, McLoughlin & Hill, 1995

♦ *Nothofagus alpina* (Poepping & Endlicher, 1838) A.S. Ørsted, 1871

Nothorhacopteris argentinica (Geinitz, 1876) Archangelsky, 1983

Osmundacidites wellmanii Couper, 1953

Ottokaria bullata McLoughlin, 1995

Otozamites linearis Halle, 1913

Ovalipollis Krutzsch, 1955

Pagiophyllum amanguanus McLoughlin & Pott, 2009

Paracalamites australis Rigby, 1966

♦ *Persoonia* Smith, 1798

♦ *Petrophile* R. Brown ex Knight, 1810

Phyllocladidites mawsonii Cookson, 1947 ex Couper, 1953

Plicatipollenites Lele, 1964

Potonieisporites Bhardwaj, 1954

Proteacidites adenanthoides Cookson, 1950

Proteacidites annularis Cookson, 1950

Proteacidites carobelindiae Milne, 1998

Proteacidites cirritulus Milne, 1998

Proteacidites concretus Harris, 1972

Proteacidites cumulus Stover & Partridge, 1982

Proteacidites palisadus Couper, 1953

Proteacidites punctiporus Macphail, Truswell & Partridge, 1993

Proteacidites reticulatus Cookson, 1950

Protohaploxypinus samoilovichii (Jansonius, 1962) Hart, 1964

Psomospora detecta Playford & Helby, 1968

Ptilophyllum acutifolium Morris (in Grant, 1840)

Ptilophyllum cutchense Morris (in Grant, 1840) emend. Bose & Kasat, 1972

Punctatisporites gretensis Balme & Hennelly, 1956

Raistrickia accincta Playford & Helby, 1968

Raistrickia corymbiata Playford in Playford & Mory, 2017

Raniganjia minima Rigby, 1966

Reticulatisporites magnidictyus Playford & Helby, 1968 emend. Playford, 2017

Retispora lepidophyta (Kedo, 1957) Playford, 1976

Retitriletes circolumenus (Cookson & Dettmann, 1958) Backhouse, 1978

Retitriletes clavatoides (Couper, 1958) Döring, Krutzsch, Mai & Schulz, 1963

Rimaesporites Leschik, 1956

Rhabdosporites langii (Eisenack, 1944) Richardson, 1960

Samaropollenites speciosus Goubin, 1965

Secarisporites Neves, 1961

Spelaeotriletes ybertii (Marques-Toigo, 1970) Playford & Powis, 1979

Sphenophyllum morganae McLoughlin, 1992

Sphenophyllum rhodesii Rigby, 1966

Sphenopteris Sternberg, 1825

Staplinisporites caminus (Balme, 1957) Pocock, 1962

Taeniopteris daintreei McCoy, 1874

Tetrahedraletes medinensis Strother & Traverse, 1979 emend. Wellman & Richardson, 1993

Velamisporites cortaderensis (Césari & Limarino, 1987) Playford, 2015

Velatitetras laevigata Burgess, 1991

Vertebraria australis McCoy, 1847 emend. Schopf, 1982

Verrucosisporites quasigobbettii Jones & Truswell, 1992

Verrucosisporites scurrus (Naumova, 1953) McGregor & Camfield, 1982

◊ *Veryhachium* Deunff, 1954

♦ *Welwitschia mirabilis* Hooker, 1862

♦ *Xylomelum occidentale* R. Brown, 1830